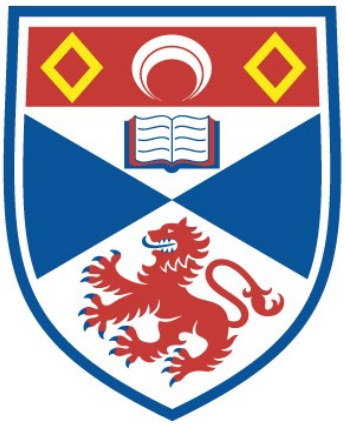
PREDATOR-PREY INTERACTIONS BETWEEN GREAT BLACK-BACKED GULLS (LARUS MARINUS) AND PUFFINS (FRATERCULA ARCTICA L.), AND THE EVOLUTIONARY SIGNIFICANCE OF PUFFIN GROUPING BEHAVIOUR

G. Kenneth Taylor

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews



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ABSTRACT

The aims of this study were to quantify various aspects of predator-prey interactions between Great Black Backed Gulls (Larus marinus) and Common Puffins (Fratercula arctica L.) in order to assess the possible long term effects of predation by gulls on a single Puffin colony and to examine the possible influence of avian predators on Puffin social behaviour.

There has been little quantification of the extent of Great Black-Backed Gull predation of Puffins throughout the gull breeding season. Chapter One extends data already published on gull predation of Puffins on the island of Dun, St Kilda, by showing what proportion of gull diet comprised Puffins and by indicating the importance of Puffin prey to gull breeding success.

Chapter Two describes the ranging behaviour and hunting success of gulls on Dun. Gulls only hunted flying Puffins, and concentrated their hunting efforts in areas near, but not directly over, their own nests. Any one pair of gulls shared on average about one third of its hunting range with two or three other pairs. Gulls attempted to catch Puffins most often in areas where Puffins, flying in polarised flocks termed 'wheels', habitually turned in to fly over land or out to fly over the sea. With increasing numbers of Puffins in a wheel, gulls made fewer attempts to catch Puffins and took longer to make a successful kill.

The grouping behaviour of Puffins is one of the most striking features of the species' social life at the breeding colony. Chapter Three describes and quantifies temporal and spatial aspects of Puffin grouping behaviour at a variety of colonies. Differences in the diurnal phasing of the formation of different types of Puffin groups, and

Abstract (cont.)

regularities in the spatial distribution of groups in the sea and in the air indicate that individual Puffins regularly synchronised some of their movements in and around the breeding colony with numbers of other Puffins breeding in or using the same part of the colony. The flight behaviour of an individual Puffin in a wheel flock above a sub-colony was influenced by the number of other Puffins in the wheel, b. wind speed and direction, and by the presence of a hunting gull in the vicinity of the wheel.

To conclude, the implications of the present study for the management, monitoring and future study of Great Black-Backed Gulls and Puffins are outlined.

February 1982.

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PREDATOR - PREY INTERACTIONS BETWEEN GREAT BLACK - BACKED GULLS (*Larus marinus*) AND PUFFINS (*Fratercula arctica* L.) AND THE EVOLUTIONARY SIGNIFICANCE OF PUFFIN GROUPING BEHAVIOUR

by

G. Kenneth Taylor

A thesis submitted for the degree of

Doctor of Philosophy

at the

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February 1982

Puffins flying in part of a wheel over the Summit Slope,

Dun Puffin colony Dense Area

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SUMMARY

The aims of this study were to quantify various aspects of predator-prey interactions between Great Black-Backed Gulls (Larus marinus) and Common Puffins (Fratercula arctica L.) in order to assess the possible long term effects of predation by gulls on a single Puffin colony and to examine the possible influence of avian predators on Puffin social behaviour.

The Great Black-Backed Gull is the largest species of gull breeding in the Northern Hemisphere. It is widely recorded as a Puffin predator, but aside from studies on the islands of Skomer, Wales and Dun, St Kilda, there has been little quantification of the extent of such predation throughout the gull breeding season. Chapter One extends data already published on gull predation of Dun Puffins by showing what proportion of gull diet comprised Puffins and by indicating the importance of Puffin prey to gull breeding success.

Puffins comprised the bulk of food eaten by all pairs of gulls monitored on Dun. Differences in the number of Puffins killed by different pairs of gulls during the incubation period were related to differences in breeding performance, with pairs which killed fewest Puffins raising fewest young. The pattern of gull nest spacing, and geographical differences in the extent of predation on young Puffins and other seabirds suggests that gulls hunted mainly near their own nests, and possibly defended these hunting areas against pairs from other nests.

Chapter Two describes the ranging behaviour and hunting success of gulls on Dun. Gulls only hunted flying Puffins, and concentrated their hunting efforts in areas near, but not directly over, their own nests. Any one pair of gulls shared on average about one third of its hunting range with one or two other pairs. Simultaneous hunting of the same area by gulls from different pairs was not observed, and the form and

outcome of agonistic encounters between gulls suggested that ownership of hunting areas was determined early in the breeding season. Gulls attempted to catch Puffins most often in areas where Puffins, flying in polarised flocks termed 'wheels', habitually turned in to fly over land or out to fly over the sea. With increasing numbers of Puffins in a wheel, gulls made fewer attempts to catch Puffins and took longer to make a successful kill. In periods when relatively high numbers of Puffins were flying above the colony gulls virtually stopped hunting.

Taken together, data in Chapters One and Two indicate that the number of gulls which attempted to breed on Dun during the study period was close to the number which could successfully raise young on a diet of Puffins. To conclude these chapters, literature on the hunting behaviour of other vertebrate predators is discussed in relation to the hunting behaviour of gulls on Dun.

Puffins typically breed in large colonies comprising several thousand to several hundred thousand individuals. The grouping behaviour of Puffins is one of the most striking features of social life at these colonies. Chapter Three describes and quantifies temporal and spatial aspects of Puffin grouping behaviour at a variety of colonies to assess whether individual Puffins attempted to synchronise their movements to, from and within the breeding colony with the movements of other Puffins. Differences in the diurnal phasing of the formation of different types of Puffin groups, and regularities in the spatial distribution of groups in the sea and in the air indicate that individual Puffins regularly synchronised some of their movements in and around the breeding colony with numbers of other Puffins breeding

in or using the same part of the colony. The spatial distribution of 'wheel' flocks of Puffins above sub-colonies reflected the distribution of breeding burrows under the wheels. The number of wheels above a colony was thus in part related to discontinuities in suitable Puffin breeding habitat. The flight behaviour of an individual Puffin in a wheel was influenced by the number of other Puffins in the wheel, by wind speed and direction and by the presence of a hunting gull in the vicinity of the wheel. Data from photographs of Puffins wheeling with and without a hunting gull in the vicinity show that Puffins in a wheel tended to bunch in response to such a predator. The extent of this bunching was positively correlated with the number of Puffins in a standard air space.

Puffins also tended to form groups away from the colony when returning from fishing grounds. Data on the behaviour of these groups are used to criticise previous interpretations of some aspects of Puffin behaviour at colonies. The behaviour of a variety of other vertebrate and invertebrate prey species in response to predators is then discussed in relation to data on Puffin groups presented in Chapter Three.

To conclude, the implications of the present study for the management, monitoring and future study of Great Black-Backed Gulls and Puffins are outlined.

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Thanks first of all to my supervisors, Dr. R.G.W. Prescott and Dr. M.P. Harris, for advice and encouragement throughout this study. Dr. Harris gave invaluable advice on fieldwork techniques, and allowed me to 'share' data from gull middens in 1977 and 1978.

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I thank the Army for allowing me to use their landing craft on journeys to and from St Kilda, and the officers and men of the Royal Artillery Detachment on Hirta for allowing me to use some of their camp facilities (the bar). The many National Trust for Scotland parties who were on Hirta during my stay were very hospitable. Graham Tiso, Eden Kinneil and Gordon Ridley generously provided boat transport to the more challenging islands and stacs of the Kilda group. Stuart Murray, Mary Harman and Elizabeth Ogilvie-Wedderburn were excellent company on Hirta, and helped make the summer of 1977 a memorable one.

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Mrs. Gwen Surridge typed most of the text, and Mrs. Elizabeth Murray prepared the figures. Peter Lack gave much advice on how to 'run-off' the references on the local supercomputer.

Finally, but foremost, thanks to my parents for their tireless support, discussion and encouragement throughout all my studies. This work is dedicated to them.

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INTRODUCTION

Introduction

'To eat and not be eaten' could be considered one of the fundamental principles structuring the life of most animals. For animals which live in groups, predation can be a selective force influencing social behaviour, such pressure from predators being considered by some to be one of the 'prime movers' of social evolution (Wilson 1975). Understanding the nature and extent of predation suffered by a social species can thus be a means of understanding some aspects of that species' behaviour. Conversely, since predator hunting strategies are likely to co-evolve with anti-predator adaptations of prey (see Harvey and Greenwood 1978), studies of prey behaviour can also aid understanding of predator behaviour. Studies of predator - prey interactions thus form an important part of both community ecology and ethology.

In recent years, it has been suggested that aspects of the behaviour of some seabird species, such as the spacing out of nests, nest sanitation behaviour, and behaviour of flocks, have an anti-predator defence function (e.g. Cullen 1957, Tinbergen et al. 1962, Kruuk 1964, Patterson 1965). Ethological work on the behaviour of predators which exploit seabirds has concentrated on the behaviour of egg predators, such as various crow species (Corvidae)(Tinbergen et al. 1967, Montevecchi 1976). Most data on avian predators which exploit adult seabirds stem from ecological studies which quantify diet but give little information on predator behaviour (e.g. Beebe 1960).

The Puffin (Fratercula arctica L.) is possibly the most

numerous Palearctic seabird (Harris 1976a). The majority of Puffins breed in large colonies comprising several thousand to several hundred thousand individuals. Puffins have a rich and varied social behaviour (see Appendix 1). Published accounts of Puffin behaviour are largely descriptions of the variety of postures and group behaviours exhibited by Puffins at their breeding colonies. The most detailed descriptions are those of Perry (1940), Lockley (1953) and Myrberget (1962). There has been little quantification of Puffin behaviour aside from data on seasonal changes in the frequency of certain types of behaviour and the behaviour of Puffins at communal grouping sites (Nettleship 1972, Taylor 1976). Puffins are subject to predation from a number of species at their colonies. The major predators of adult Puffins are man, the Great Black-Backed Gull (Larus marinus) and Great Skua (Catharacta skua) (Lockley 1953, Anderson 1976, Nørrevang 1977, Furness 1979). The most important of these in Britain is the Great Black-Backed Gull, which is widely recorded as a Puffin predator at colonies where the two species breed in close proximity.

The Great Black-Backed Gull is the largest gull breeding in the Northern Hemisphere. In recent decades it has expanded its breeding range and increased in numbers on both sides of the Atlantic (Harrison and Hurrell 1933, Gross 1945, Davis 1958, Parslow 1967, Burger 1978, Møller 1978). The British population was estimated to be in the region of 22,000 pairs in 1969-70, the largest concentration of breeding pairs being in north and west Scotland (Cramp et al. 1974). Various authors have expressed concern that the predatory activities of L. marinus may have a detrimental effect on the breeding

stocks of Puffins at some sites where the two species breed, or otherwise feared that gulls may kill many thousands of the Puffins at a single colony each year (Darling 1939, Williamson 1958, Tuck and Heinzel 1978). One such site where gulls have long been recorded killing Puffins is the island of Dun in the St Kilda group of the Outer Hebrides.

Given this background, the aims of the present study were:

To quantify the diet of Great Black-Backed Gulls breeding on Dun to assess what proportion of gull diet consisted of adult, immature and fledgeling Puffins.

To monitor the breeding sucess of gulls nesting in high and low Puffin burrow density areas of Dun, and assess whether differences in gull breeding performance were associated with differences in nest position and diet.

To document the ranging behaviour and intra-specific interactions of gulls hunting Puffins to determine whether gulls defended hunting territories, and if so, to assess the maximum number of gull pairs which could hunt Puffins on Dun.

To quantify the hunting success and behaviour of gulls attacking Puffins in flocks of different densities to assess whether hunt success was affected by changes in prey density.

To quantify various aspects of Puffin group behaviour, and assess the influence, if any, of aerial predators and kleptoparasites on group structure to determine whether joining a group might reduce an individual Puffin's risk of predation or of losing food.

Using data from all of the above, the study thus aimed to assess both the influence of Great Black-Backed Gull predation on Puffins under present levels of predator and prey

on Dun, to suggest how changes in predator or prey numbers on Dun would influence this predation, and to indicate the possible influence of predation and kleptoparasitism on the evolution of Puffin social behaviour.

Principal Study Sites

The geographical position of study sites is indicated in Fig 1.

Dun (57° 48'N, 8° 34' W) (Plate 1, Fig 2) is the fourth largest island in the St Kilda group of the Outer Hebrides, Scotland. Descriptions of the physical and biological features of Dun and other islands in the group are given in the accounts of Williamson and Boyd (1960) and Jewell et al. (1974). Dun is 1.4 Km long and rises to a height of 183 m a.s.l. at its summit. The island is cliff bound along its south western side and difficult of access, crossings to the island during the present study being made in a breeches buoy suspended from a steel cable stretched across the Dun Gap. The north western side of Dun which flanks Village Bay is vegetated and slopes steeply, mostly at an angle of 30° or more. The two main vegetation types are rank Festuca grassland and bird-influenced Rumex sward. The main breeding concentrations of Puffins are on this side of the island. Data on population size, burrow distribution and breeding biology of Puffins breeding on Dun in the period 1974-1980 are given in the works of Harris and Murray (Harris and Murray 1977, 1978, 1981, Harris 1980, 1981). These authors distinguished two large areas of Dun with grossly different Puffin burrow density. They called the high burrow density area, on and to either side of the summit slope, the Dense area, and the

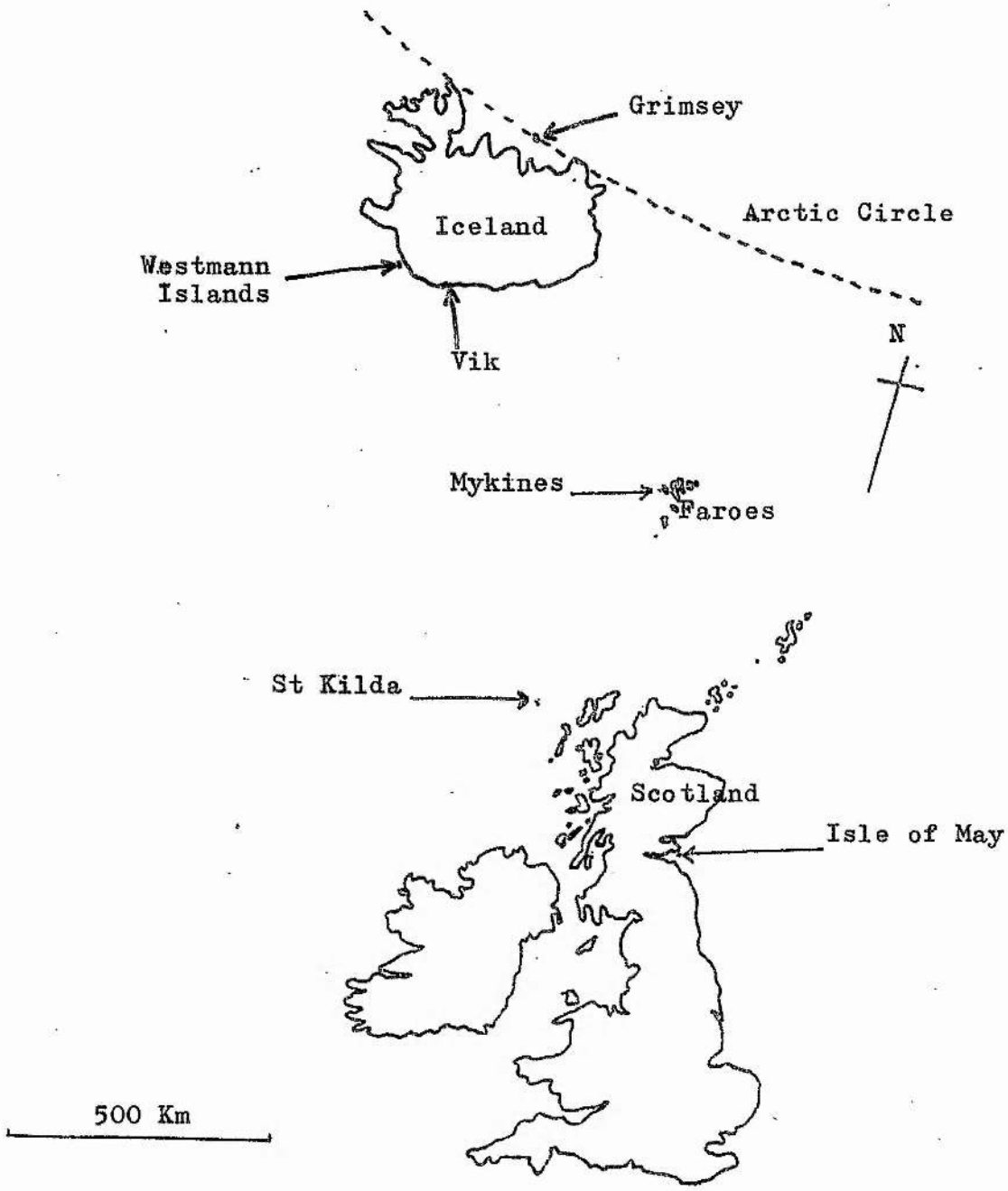


Fig. 1 Geographical position of study sites (arrowed)

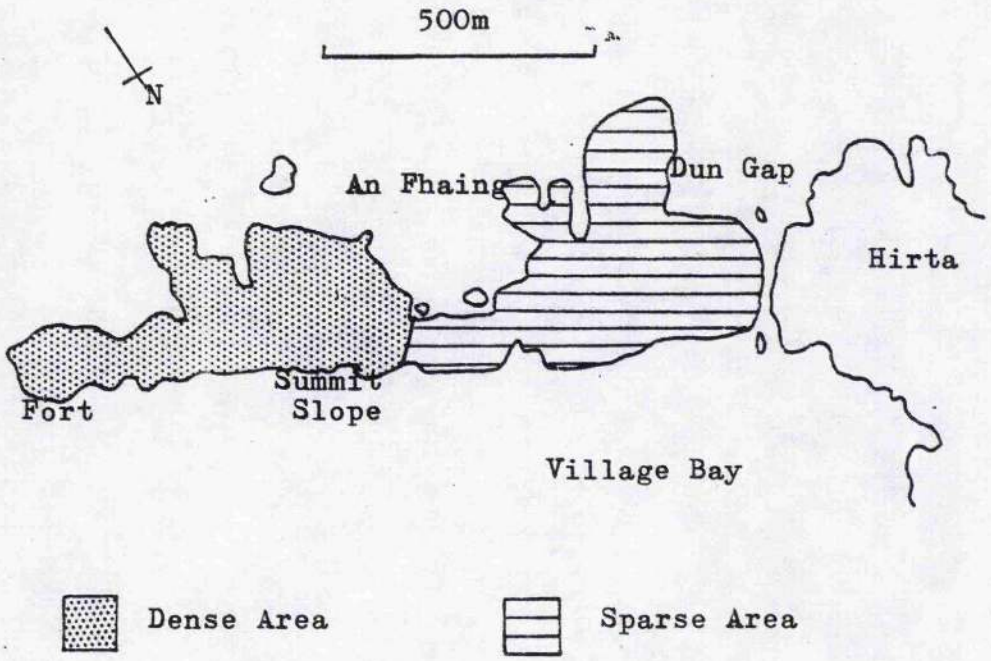


Fig. 2 The island of Dun and part of Hirta

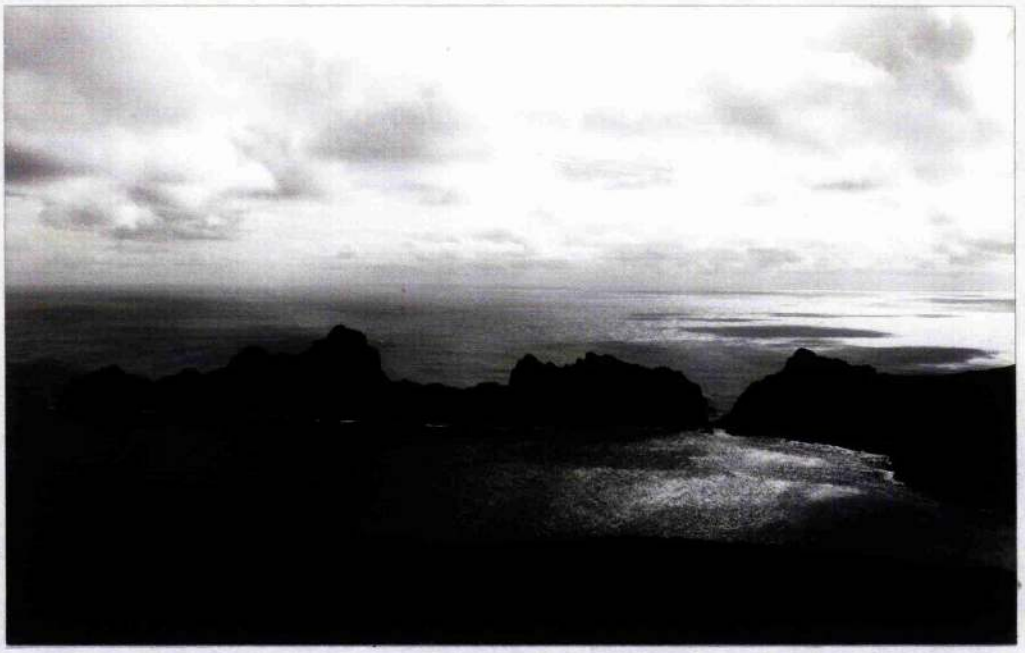


Plate 1 The island of Dun seen from Hirta

low burrow density area in the north western part of the island the Sparse area (Fig. 2). These terms will be used in this study to refer to these two areas of the Dun Puffin colony. The only quantitative information on predation of Puffins by gulls on Dun for years prior to and during the present study is given in Harris (1980).

The Isle of May (56° 10' N, 2° 35' W) (Plate 2, Fig. 3) lies 10 Km off the coast of Fife in the mouth of the Firth of Forth, Scotland. The island is approximately 1.6 Km long by 0.5 Km wide and rises to a height of 46 m. a.s.l. It has a rocky coastline, with cliffs along much of its south western side. Descriptions of the island's physical and biological features are given by Eggeling (1960).

Puffins now breed in many parts of the Isle of May, the number of breeding pairs having increased dramatically in the last two decades from around ten pairs in the 1950's to in excess of 10,000 pairs at present (Harris 1977, 1981, Harris and Murray 1981). The main concentration of breeding Puffins on the island is in the Burrian area. Adult Puffins are largely free from predation on the Isle of May. One or two pairs of Great Black-Backed Gulls attempted to breed on the island during the present study, but were unsuccessful due to gull control measures carried out as part of the management of the island as a National Nature Reserve.

Other study sites

Mykines (62° 06'N 07° 35' W) (Fig. 4a) is the westernmost island in the Faroes. It has a cliff bound coastline, and rises to a height of 560 m. a.s.l. Descriptions of physical and biological features of the island are given by Pedersen

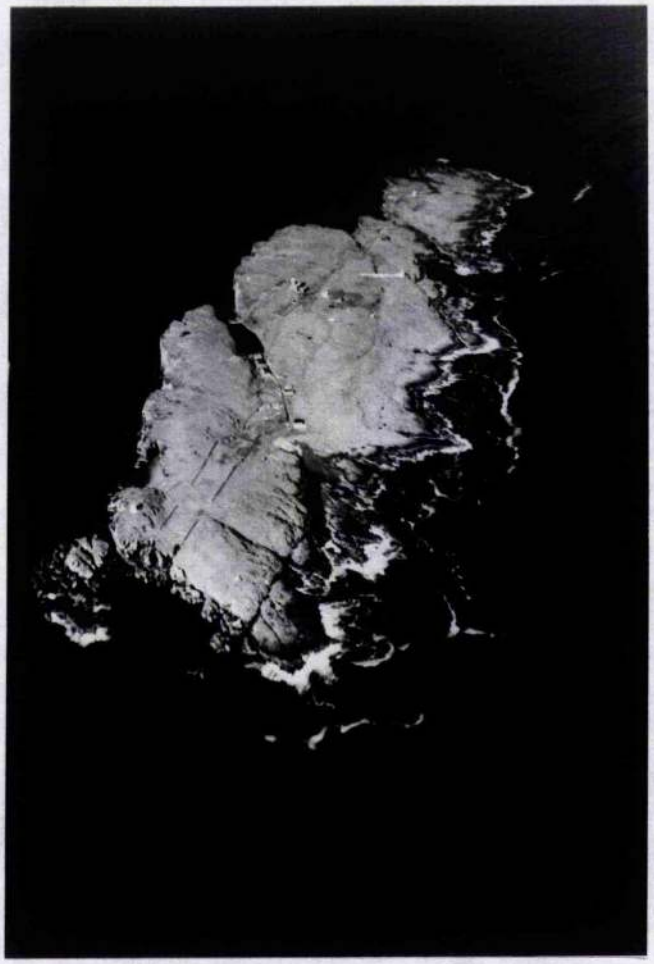


Plate 2 The Isle of May

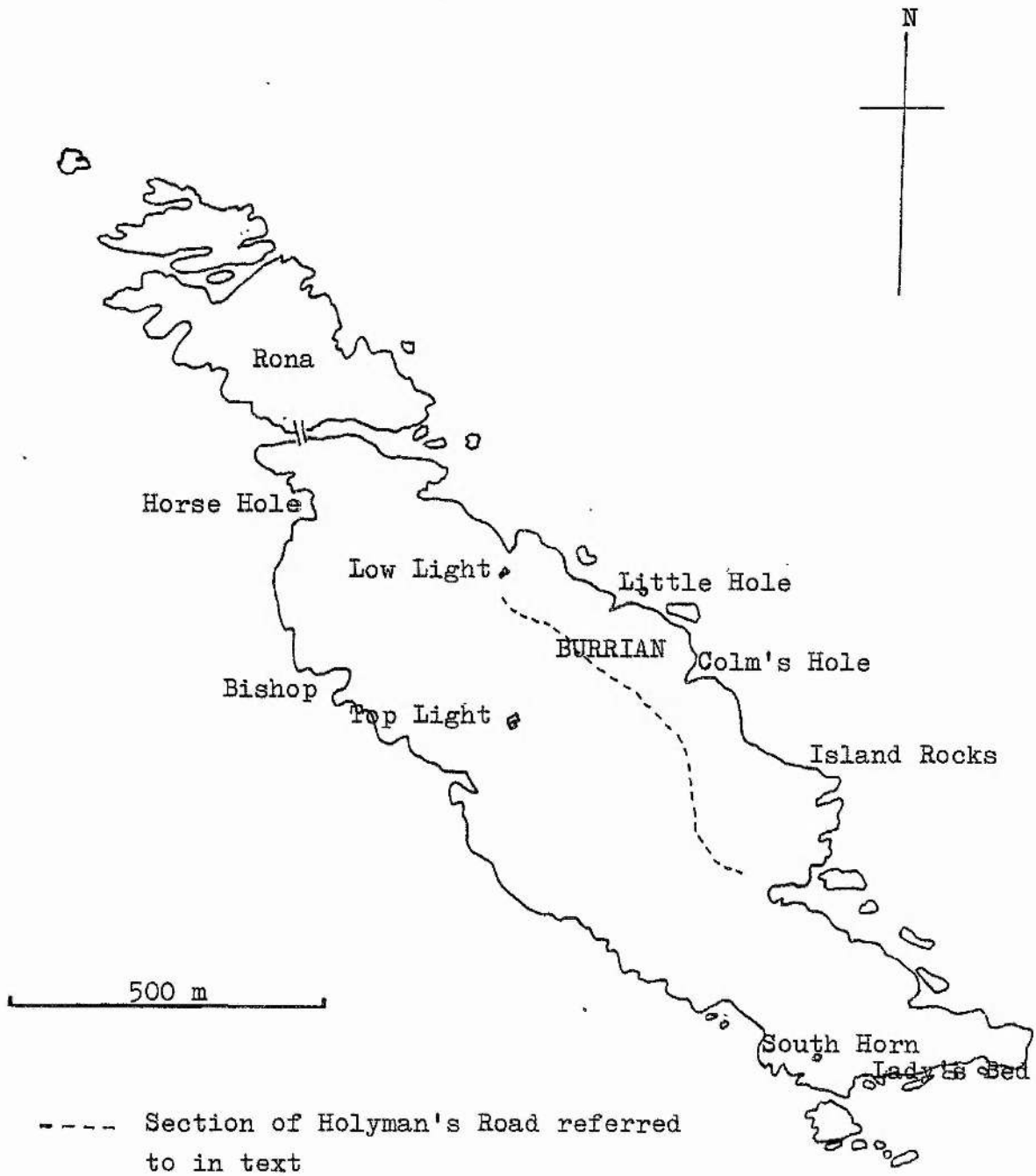


Fig. 3 The Isle of May

(1935), Williamson (1948) and Nørrevang (1977). The largest concentrations of breeding Puffins on Mykines are in the area between the hamlet Mykinesbygd and the holm Mykinesholmur. Puffin burrow densities in this area are among the highest recorded anywhere in the world (Taylor 1981). The total population of breeding Puffins on Mykines was of the order of 100,000 pairs in the 1930's (Pedersen 1935). The principal Puffin predator on Mykines is man, fowlers catching tens of thousands of young and adult Puffins annually (Nørrevang 1977).

Heimaey (63° 25' N 20° 17' W) (Fig. 4b) is the only inhabited island in the Westmann group off Iceland's south coast. It is approximately 3.2 Km long by 2.5 Km wide and rises to a height of 227 m. a.s.l. General descriptions of the island's inhabitants and seabird populations are given by Lockley (1938). Data on Westmann Island Puffin biometrics are given by Pedersen (1976). The island is volcanic, with two cones of a recently active volcano dominating the landscape. Observations of Puffins on Heimaey made during the present study were mainly of birds breeding on the slopes of an old crater around Herjolfur's Valley.

Vik i Myrdal (63° 25' N 19° 00'W) (Fig. 4c) is a small township near the southernmost point of the Icelandic mainland at the mid-point of the south coast. Puffins breed inland about 1.5 Km from the centre of township in both east and west directions. Observations during the present study were made at the East Colony, a site separated from the sea by about 1 Km of glacial outwash beach. The habitat and burrow distribution of this East Colony, referred to in this study as the 'East Cliff' colony have been quantified by Grant and

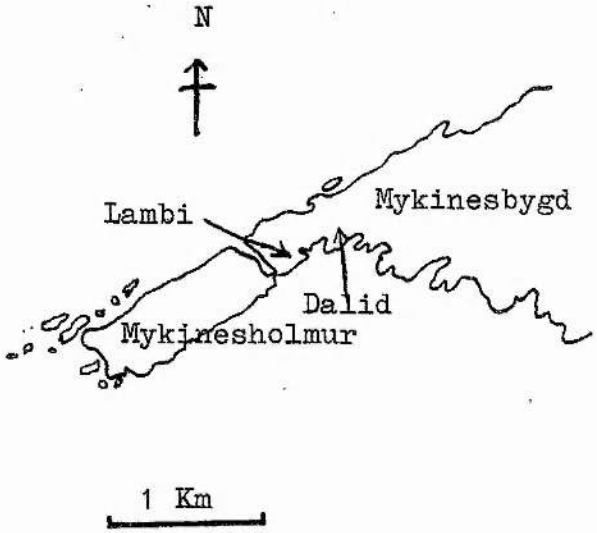


Fig. 4a Part of Mykines, Faeroe Islands (after Williamson 1948)

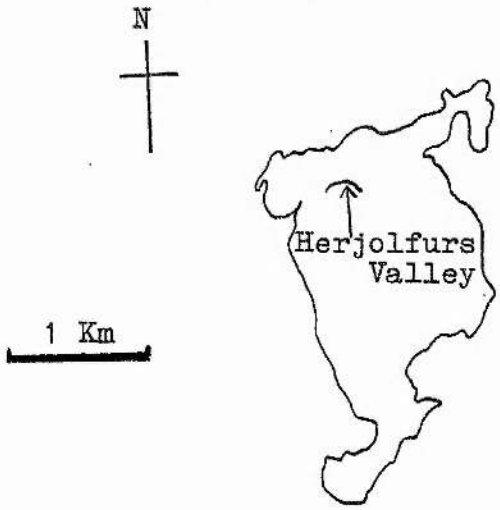


Fig.4b Heimaey, Westmann Islands (after Lockley 1938)

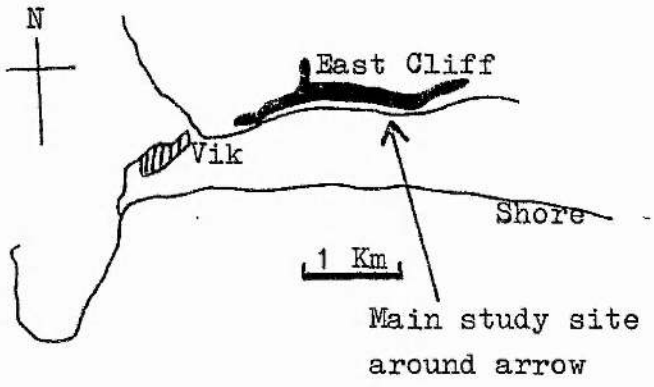


Fig. 4c Vik i Myrdal and East Cliff Puffin Colony, Iceland (after Arnason and Grant 1978)

Nettleship (1971).

Puffins flying in to the East Cliff with fish to provision young are attacked by a variety of avian kleptoparasites, principally the Arctic Skua (Stercorarius parasiticus) and Herring Gull (Larus argentatus). Interactions between Puffins and kleptoparasites at this site have been documented in a number of papers (Grant 1971, Arnason 1978, Arnason and Grant 1978, Taylor 1981).

Grimsey (66° 33' N 18° 00' W) is a small island lying on the Arctic Circle 42 Km from the nearest point on the Icelandic mainland. The breeding bird populations of Grimsey have been described by Foster et al. (1951). The island has cliffs on its east side, the west coast being almost flat with several small irregular bays. A narrow rocky beach skirts the island almost everywhere below the cliffs, and the interior is a gently sloping rough pasture grazed by horses. Although the Grimsey villagers used to kill thousands of Puffins and other seabirds annually for food, the extent of this predation is now much reduced, fowling being more a hobby than a necessary part of the villagers' livelihood. Puffins on Grimsey breed principally in boulder piles on the beaches, and on the upper parts of cliffs where there is some soil. Given the nature of the breeding habitat, the Puffin population can only be guessed, on the basis of my field notes, as being in the order of several tens of thousands of pairs. Aside from man, Great Black-Backed Gulls also prey on Grimsey Puffins, but the gulls are themselves killed where possible by villagers.

Definitions

Throughout this study 'gull' refers solely to the Great

Black-Backed Gull and 'Puffin' to the Common Puffin unless otherwise stated.

Statistical methods

Non-parametric statistical methods are taken from Siegel (1956). Parametric statistical methods are from Bailey (1959). Means are given $\pm$ standard error unless otherwise stated.

CHAPTER ONE

Feeding ecology and breeding success of *Larus marinus* breeding on the island of Dun, St Kilda

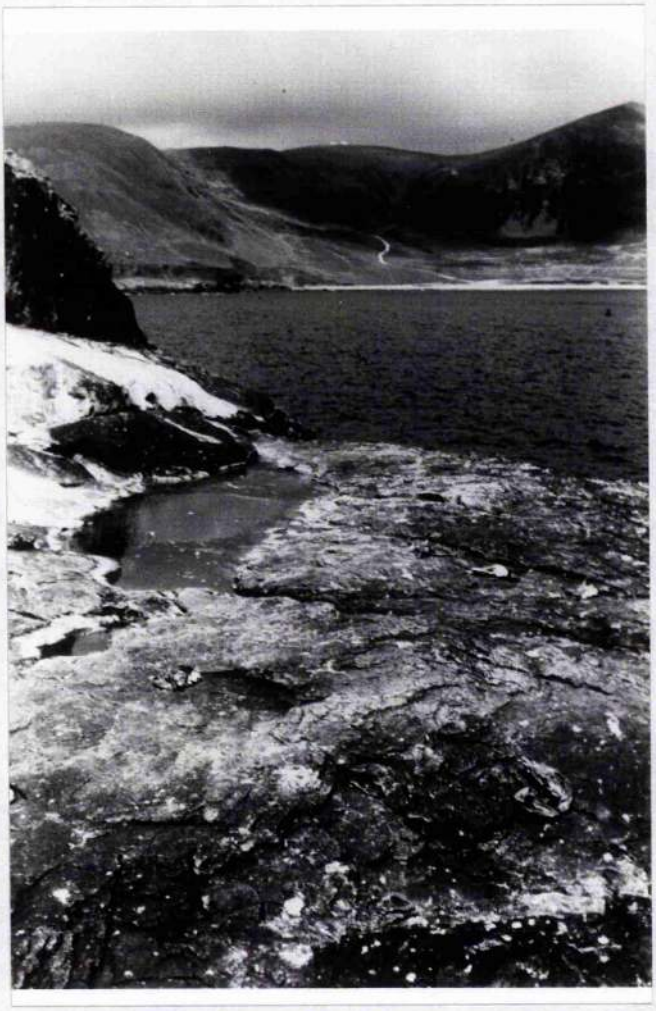


Plate 1.1 Midden used by gulls from Nest 8, Dun Dense Area

"Nothing comes amiss to it. It is omniverous.... Along the shores and cliffs it is, when it has young, and abiding terror to the fulmars, puffins, guillemots, terns and plovers."

Percy R. Lowe 'Our Common Sea-Birds' London, 1914

INTRODUCTION

The breeding population of L. marinus on Dun

L. marinus has bred on St Kilda since records started, Martin (1698) referring to it as the largest species of 'sea-mall' nesting there. It has frequently been mentioned in accounts of St Kilda breeding birds, but estimates of the breeding population before 1973 are fragmentary in their coverage of the various islands in the group (e.g. notes in Macaulay 1764, Gray 1871, Harvie-Brown and Buckley 1888, Heathcote 1900, Clarke 1912, Harrison and Lack 1931, Baxter and Rintoul 1953, Williamson and Boyd 1960).

During the period when the St Kilda village on Hirta was occupied, the villagers relied on harvesting seabirds and eggs for their subsistence (Steel 1975). L. marinus was considered a competitor for this food, particularly because it was seen killing Puffins and stealing Fulmar (Fulmar glacialis) eggs (Wiglesworth 1903). Consequently, the Kildan villagers went to great lengths to destroy L. marinus nests and kill young and adult gulls (Macaulay 1764, Elwes 1869). Since the evacuation of villagers in 1930, Dun has been relatively free of human disturbance. In 1939 'a few' L. marinus nests were found on Dun, 'but the breeding strength was evidently quite small' (Nicholson and Fisher 1940).

Since 1973, annual counts of L. marinus nests have been made on the island of Dun (Harris and Murray 1977, Harris 1980). These counts appear to indicate an increase in the

number of pairs breeding on Dun after 1973, reaching a peak in 1977 when forty pairs nested. However, Harris and Murray (op. cit.) thought that this may have been an artefact of their increasing interest in the species and familiarity with the island, the population probably having remained stable at between thirty and forty pairs over the past few years. The L. marinus population on the island during my study period was thus likely to have been higher than that during several centuries up to the 1930's.

The diet of Dun gulls

There is no quantitative information on the diet of L. marinus on St Kilda before the 1970's. General descriptions of some of its feeding habits, such as egg stealing and Puffin predation, and notes on unusual feeding circumstances are given by a few authors (Wiglesworth 1903, Atkinson 1949, Williamson 1958, Boddington 1959, Williamson and Boyd 1960).

From 1975 to 1978, c. 2,600 Puffins were killed annually by L. marinus on Dun (Harris 1980). Most predation occurred between late April and late July in each year. It was estimated that L. marinus predation was responsible for an annual loss of c. 1.5% of breeding Puffins on Dun. However, birds nesting in low burrow density areas suffered a higher mortality (4.2% of adults) than birds in high burrow density areas (0.9% of adults).

Scope of the present study

The work of Harris (1980) gives a means of assessing the effect of L. marinus predation on adult Puffins under present levels of predator and prey. The present study provides

data on the contribution of different species and age-classes of prey to gull diet to allow assessment of how these species are affected by L. marinus predation throughout the breeding season. These data, and information on L. marinus nest spacing and breeding success, provide a background to data on hunting behaviour presented in Chapter Two, extend previous accounts of L. marinus diet and hunting behaviour, and provide a framework for assessing the possible effect of future L. marinus predation on Puffins on Dun and elsewhere.

Methods

In 1977 and 1978, all gull nests were plotted on 1:4310 maps. Some nests were inaccessible but visible from the sea, and few, if any nests were thought to have been overlooked. The spatial distribution of gull nests was analysed using methods described in Section 1.1.

Gulls on Dun habitually used sites, referred to here as 'middens', as processing areas for captured prey. Middens were usually located on rocks which held a rainwater pool or pools, although some middens were found in grassy depressions which only occasionally contained water. Water appeared to help the gulls skin avian prey. Corpses were usually left at middens after gulls had eaten, food picked from carcasses being fed to chicks by regurgitation at the nest. A typical midden site is illustrated in Plate 1.1.

Middens were plotted on gull nest maps and nests and middens inspected by myself about every seven to ten days during most of the gull breeding season in 1977 and during June 8 to July 9 1978. Further clearances in 1978 were made by S. Murray in May and August. Thirteen clearances were

made between 15 May and 9 August 1977 and eight between 15 May and 5 August 1978. Food remains were itemised at each inspection and then destroyed.

The number of grooves on the bill sheaths of Puffin corpses was recorded where possible. (Grooves allow adult and immature Puffins to be differentiated. Immature birds of four years old or younger have two or fewer bill grooves. Most adult Puffins have more than two bill grooves, (Ashcroft 1976, Harris in press).

Scattered parts of corpses, such as detached wings, heads and feet, were classed as parts of ageable corpses where detached heads with bill sheaths were found, and as 'bits'. The number of bits recorded for any one midden visit was calculated as the smallest number of complete Puffin corpses which could include all the parts found after detached heads with bill sheaths had accounted for some or all of the remains. For example, three pairs of wings, four feet, one sheathless head and two heads with sheaths would be recorded as two corpses of known groove class and one bit.

Where the remains of Puffin chicks and of adults and young of other species consisted of regurgitated boli with feet, the corpse tally for a given species and age class was calculated by counting the number of feet and dividing by two. Feet and feathers were identified to species and age class by reference to intact corpses of seabirds found on Dun.

Food remains were also itemised at middens on nearby Hirta, Boreray and Soay, and at Vik and Grimsey in Iceland for comparison with Dun middens.

A measure of the accuracy of midden clearance as an estimate of gull predation on Puffins is presented in Chapter Two,

where data on gull hunt frequency and hunt success are used to assess the match between the expected number of Puffins killed during part of the gull nestling period and the number of Puffins found at middens. A measure of corpse survivorship at middens was obtained by marking 71 fresh Puffin corpses at 17 different middens on 3 July 1977 with white plastic rings fitted tightly to right or left carpal joints. These marked corpses were left where found, and their survival at the 17 middens recorded until the last clearance of the season on 9 August 1977.

1.1 DISTRIBUTION OF GULL NESTS

Data on the location of gull nests on Dun in 1977 and 1978 are presented here to describe nest site habitat characteristics. Nearest neighbour statistics are used to quantify the distribution of nests and assess whether nests were clustered, randomly sited, or spaced out relative to other nests.

Methods

Distances between each nest and its nearest neighbouring nest were measured from nest maps and used to generate the nearest neighbour statistic R_N (Clark and Evans 1954). Derived from work in plant ecology, R_N describes the dispersion pattern of static points, and indicates the direction and magnitude of a pattern's deviation, if any, from random spacing. Random patterns have $R_N = 1$, perfectly clustered patterns $R_N = 0$, and perfectly regular patterns $R_N = 2.1491$. Nearest neighbour distances of mapped nests were used to compute mean observed distances ($\bar{d}_O$) for the whole island. The expected spacing for a random distribution of nests ($\bar{d}_E$) was generated

by the equation $\bar{d}_E = \frac{1}{2}\sqrt{\frac{A}{n}}$ (Smith 1975) where A = the area of Dun and n = the number of nests. R_N was calculated by dividing $\bar{d}_O$ by $\bar{d}_E$

An arbitrary definition of a 'cluster' of nests, based on visual inspection of mapped nest distributions, was used for further analysis of nest dispersion. A group of nests was classified as a cluster if it contained three or more nests, all of which were reciprocal nearest neighbours, i.e. if each nest in the group was closer to all other nests in the group than it was to any single nest outwith the group.

Results

Gull nest positions in 1977 and 1978 are shown in Figs.1.1 and 1.2. Gulls tended to choose nest sites near the island's coast. Mean nest to nearest coast distance was 26.4 m. ($\pm$ 2.81) in 1977 and 24.5 m. ($\pm$ 2.9) in 1978. (The maximum possible distance from the coastline is about 130 m.) Most nests were built in short vegetation near bare coastal rock and lined with grass. Nests 30, 35, 37 and 40 were atypical, built among thick grass inland. Elevations ranged from 2 - 3 m. above sea level (nests 4, 5, 6) to about 100 m. a.s.l. (nest 38). Nests 22 and 23 were on rocky promontories with a panoramic view, and many other nests had rock columns nearby which were used as loafing sites. Most nests in 1978 were built in the same location as nests in 1977. The exception was nest 17a, built by a new pair after the failure of the adjacent nest 17 in 1978.

Nearest neighbour measures for nests in 1977 and 1978 indicate that nest dispersion across the whole island was more regular than random in both years (Table 1.1).

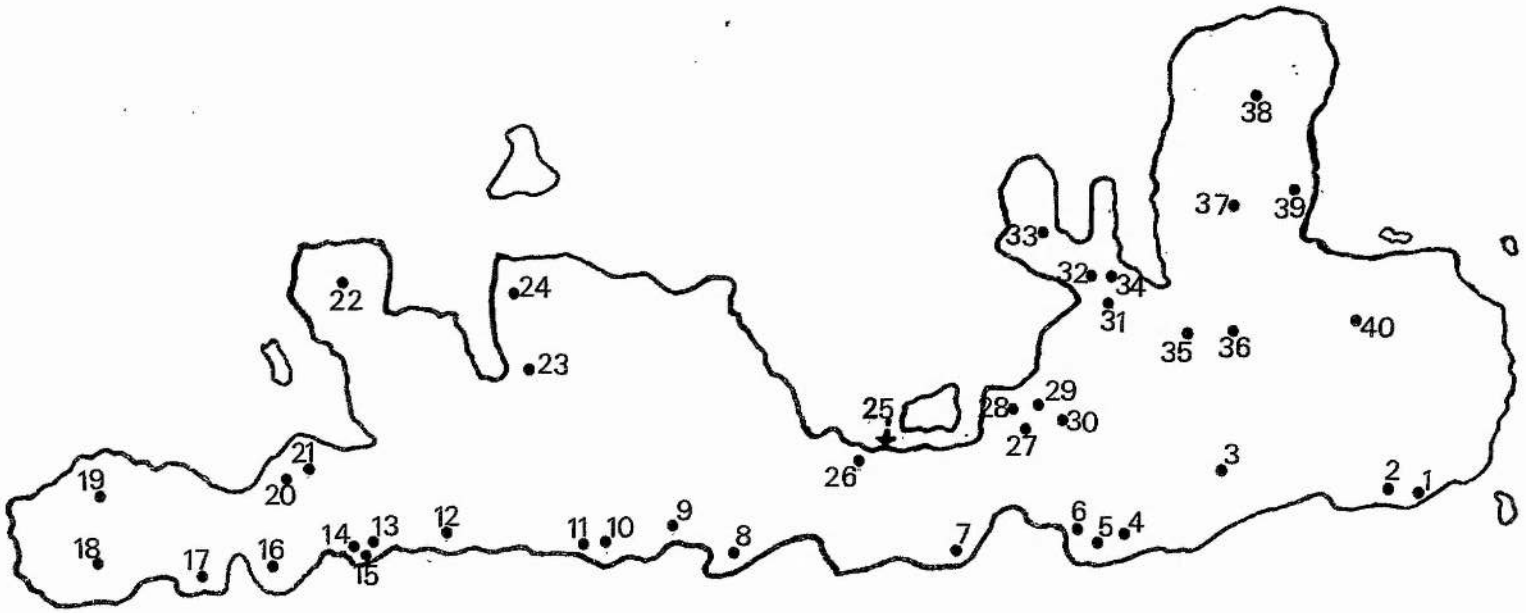


Fig. 1.1. L. marinus nests 1977

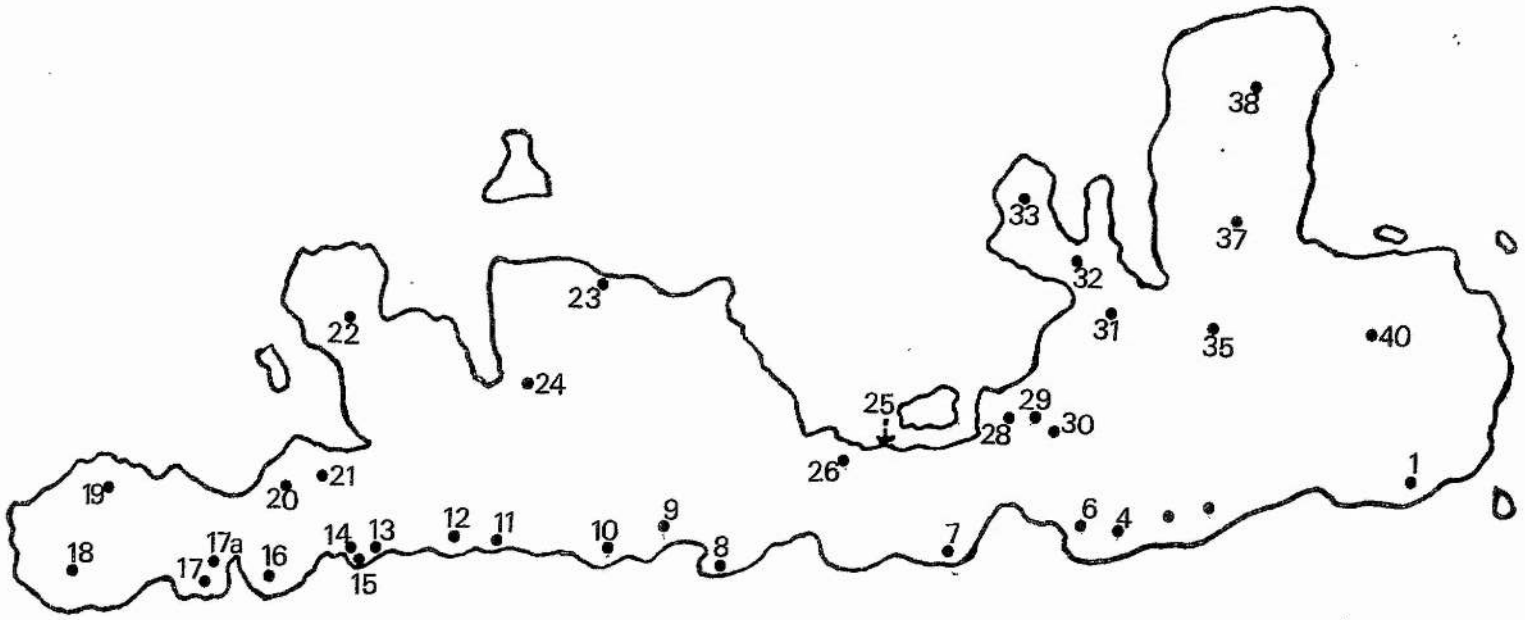


Fig. 1.2. L. marinus nests 1978

Table 1.1 Breeding density and nearest neighbour values for L. marinus nests on Dun in 1977 and 1978

Year	Area	Pairs	m^2/pair x 10^{-3}	$\bar{d}_o$ (m)	R_N	P (1-t)
1977	Sparse	21	6.95	47.9 ± 32.3	1.15	0.097
	Dense	19	7.21	54.0 ± 37.5	1.27	0.012
	Whole Island	40	7.08	50.8 ± 34.5	1.21	0.006
1978	Sparse	16	10.45	71.1 ± 43.4	1.49	<0.001
	Dense	20	6.86	50.2 ± 36.4	1.21	0.110
	Whole Island	36	7.86	59.5 ± 40.5	1.34	<0.001

The lowest and highest R_N values, for the Sparse area in 1977 and 1978, were found respectively with the highest and lowest observed nest densities. R_N values for the Dense area, and for the island as a whole, were also higher when there were least nests in these areas. That is, the less nests there were in an area, the more spaced out was their dispersion pattern in comparison to a year when there were more nests in the same area.

The highest percentage of nests located in clusters was in the Sparse area in 1977, when 47.6% of nests were clustered and the highest number of nests was found in that area (Table 1.2).

The distance between clusters and their nearest neighbouring single nests was greater than the distance between nests outwith clusters. In 1977, when the highest number of clusters was observed, single nests near clusters were sited at significantly greater distances from clusters than the distances between pairs of nests outwith clusters ($t = 2.12$ $p<0.05$ $2 - t$) .

Table 1.2 Spacing of nests (m) within and outwith clusters

Year	Area	Nests	Clusters	% clustered	$\bar{d}_0$ in cluster	$\bar{d}_0$ out cluster	$\bar{d}_0$ nearest out cluster to in cluster
1977	Sparse	21	3	47.6	25.1	59.5	96.5
	Dense	19	1	15.8	13.2	60.2	72.7
	Overall	40	4	32.5	22.5	64.1	89.9
1978	Sparse	16	1	18.8	26.4	81.3	119.0
	Dense	20	1	15.0	13.2	56.9	72.7
	Overall	36	2	16.7	19.8	68.1	87.9

Discussion

L. marinus nests are usually more widely spaced out than the nests of many smaller gulls, and the species has been described as a 'solitary' nester (Harris 1964, Butler and Tivelpiece 1981). There is considerable variation in inter-nest distances between colonies. For example, about 2,000 pairs of L. marinus nest on North Rona in an area smaller than Dun (Evans 1975, 1978).

Since nests on Dun were spaced out more than would be expected from a random occupation of the island, many Dun gulls could be considered 'territorial', following Davies' (1978) definition of territory. Since the concept of territory involves consideration of a variety of different activities for which territories can be used (Hinde 1956), it is reasonable to ask which activities might have produced the observed spacing of nests on Dun. Since gulls at other colonies, such as North Rona, successfully breed closer together than Dun gulls, it is unlikely that the distribution of Dun nests reflected territorial defence due to the species' courtship space or nesting space requirements. Given the long history of human persecution of

gulls on St Kilda, spacing out could be in part a defence against predators (cf Tinbergen et al. 1967). However, as L. marinus was widely persecuted throughout Britain up to the middle of the 19th century (Harrison and Hurrell 1933), predation is unlikely to be the sole cause of the nesting pattern on Dun.

Food is the primary resource defended in the majority of bird species for which the protected resource associated with territory is 'reasonably well established' (Wilson 1975). Reviews and mathematical models of spacing behaviour further suggest that if food is uniformly distributed, individuals should tend to space themselves out, with each foraging near its nest (Crook 1965, Horn 1968, Smith 1968, Brown and Orians 1970). On the basis of L. marinus feeding habits, Lack (1967) felt that the nesting dispersion of the species in Britain was presumably related to food supplies. By contrast, food resources which are unpredictable in time and space, such as fish shoals exploited by many seabirds, may promote colonial breeding. This type of breeding is seen in its most extreme form in the Common Guillemot (Uria aalge) which feeds on shoaling fish such as sandeels (Ammodytidae) and breeds at densities unparalleled by any other avian species (Birkhead 1978).

The idea that the nesting pattern of Dun gulls reflected defence of feeding areas on the island is supported by data on the spacing of single nests relative to clusters. If it is assumed that gulls nesting in clusters ate the same food as other gulls in and outwith clusters, and that obtaining this food required defence of an area of the island against other gulls, then a group of breeding gulls would require a larger feeding area than a single pair. This could account for the

greater distance between neighbouring single nests and clusters than between neighbouring single nests.

To assess whether food supply influenced the number and distribution of breeding gulls on Dun, detailed information on the diet of individual pairs of gulls is required. Sections to follow present such data.

1.2 SURVIVORSHIP OF CORPSES AT MIDDENS AND THE ASSOCIATION BETWEEN MIDDENS AND INDIVIDUAL PAIRS OF GULLS

Two possible sources of error in quantifying gull diet using the midden clearance technique were that I could have failed to find some corpses actually present at a midden, and that some corpses of prey killed after one clearance could have been moved from middens by gulls before the next clearance. Data on the survivorship of marked corpses left in situ at middens quantify the magnitude of such errors. Data on midden distribution and contents demonstrate the extent to which different middens could be associated with different pairs of gulls and hence the extent to which midden contents could be used to quantify the diet of individual pairs of gulls.

Results

A map of midden sites, numbered with reference to the numbering of adjacent gull nests, illustrates that most middens were situated close to individual nests (Fig. 1.3). For the two middens associated with nests 1 - 6, on tidal rocks in the Sparse area, it was not possible to link food remains found at the middens with individual pairs of gulls in 1977. In 1978, midden 1/2 was used only by the pair from nest 1, but

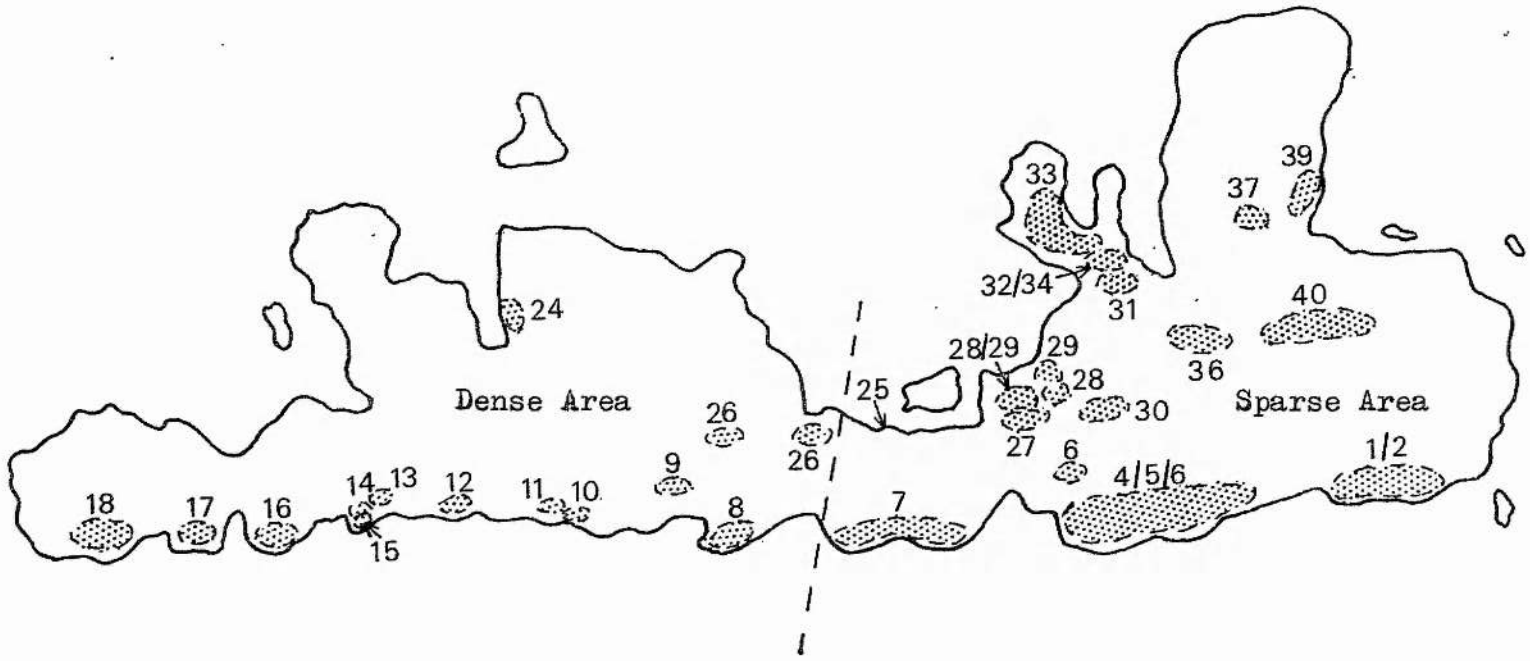


Fig. 1.3. Gull Middens on Dun 1977/1978

in this year a fourth pair shared the 4/5/6 midden.

Puffin corpses were often processed differently at different middens. For example, the majority of Puffin remains found at midden 16 were pairs of wings, in complete contrast to nearby midden 17, where most Puffin remains were carcasses with limbs still attached.

The survivorship of 71 corpses marked at Dense and Sparse middens on 3 July 1977 is illustrated in Fig. 1.4. At the end of the 38 day experiment, 18 corpses, or c.25% of the total marked, were not found. Fewer marked corpses were found at Sparse area middens than at Dense area middens, but this difference is not significant ($\chi^2 = 1.04$). In 60% of Dense area middens and 29% of Sparse area middens all corpses marked were still present at the end of the marking study.

Discussion

If different gull pairs used different techniques for processing prey, but shared middens, a variety of types of carcass would be found at each midden. If middens were not shared, different types of carcass would be observed at different middens, as was the case on Dun. Extensive data on inter-midden differences in prey remains is presented in later sections, but the evidence presented so far on prey remains and on the spatial association between nests and middens supports the idea that the contents of a single midden often represented the remains of prey captured by one pair of gulls.

Data on corpse survivorship indicates that once at a midden, the majority of corpses remained there during a period longer than the usual interval between midden clearances. Fluctuations in survivorship suggest that some corpses which

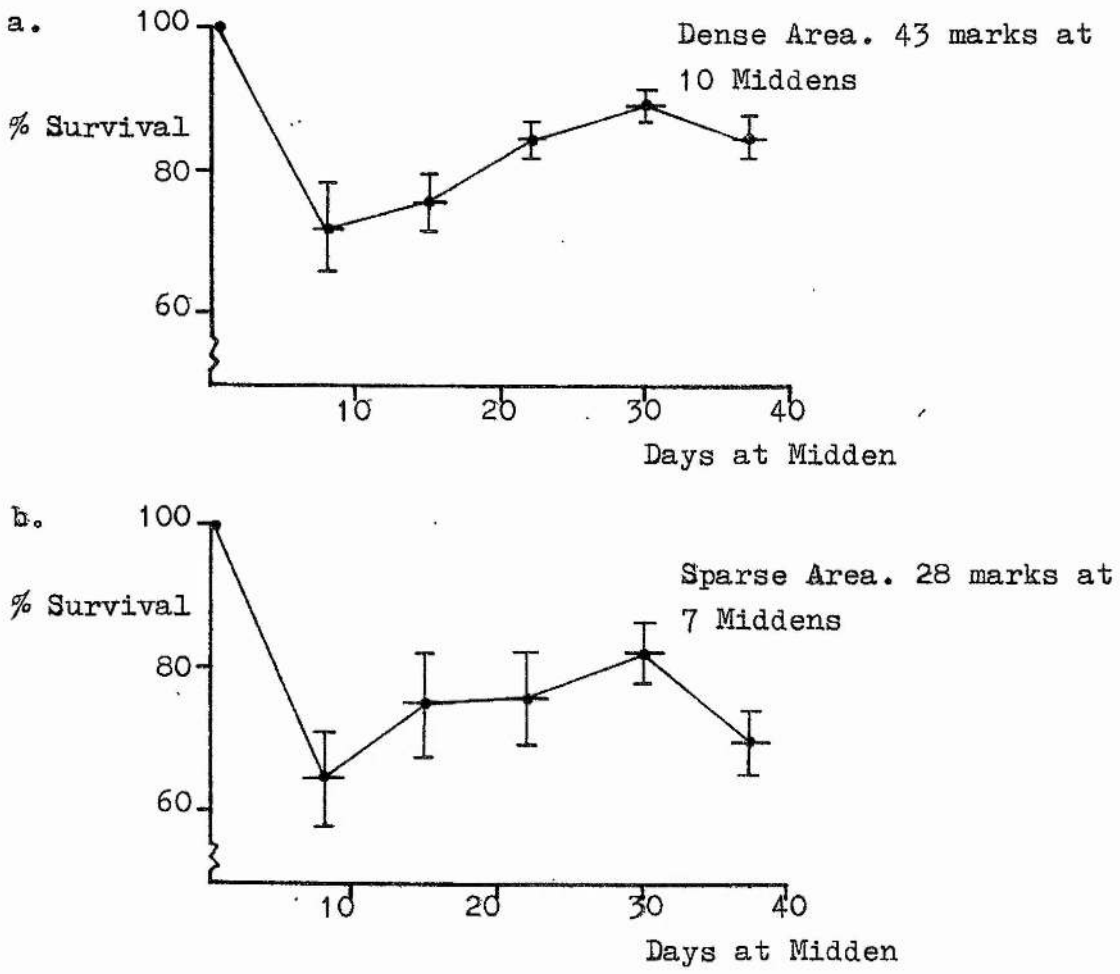


Fig. 1.4. Survival of marked corpses left at middens in 1977

were actually present at middens may have been missed during a single clearance, but that this would usually apply to fewer than 20% of corpses present at any one midden. Since corpse degeneration could have resulted in some rings being detached from marked wings, figures presented here are a conservative estimate of corpse survivorship and my corpse finding success.

1.3 THE SPECIES COMPOSITION OF FOOD REMAINS FOUND AT L. MARINUS MIDDENS

Previous studies of L. marinus food on Dun during the 1970's documented the number of Puffins killed by gulls, but did not quantify predation on other species (Harris 1980). Data presented here illustrates what proportion of all gull prey consisted of Puffins. This gives a general account of the species' diet on Dun and other St Kilda islands and provides a background to more detailed data on differences in prey selection between different pairs of gulls on Dun. Data for 1977 cover most of the gull breeding season, but data for 1978 cover only the period 8 June to 8 July. Only Puffin remains were itemised in clearances outwith this period in 1978.

Results

Puffin remains comprised over 96% of the total biomass of avian prey found at middens in both years (Table 1.3). About two percent of food was remains of non-avian prey. Some of these non-avian items, such as cooked bones and some fish bones, were obtained by scavenging at the Army camp on the neighbouring island of Hirta, and possibly contained little food usable by the gulls when found. An unknown proportion

Table 1.3. Contribution of different prey species to gull diet

	15/5 to 9/8/77		8/6/ to 8/7/78	
Adult Birds	N	% bird wt.	N	% bird wt.
Fulmar (Fulmaris glacialis)	1	0.1	1	0.2
Manx Shearwater (Puffinus puffinus)	2	0.1	1	0.1
Leach's Petrel (Oceanodroma leucorhoa)	2	0.1	2	0.1
Kittiwake (Rissa tridactyla)	2	0.1	-	-
Razorbill (Alca torda)	2	0.1	-	-
Guillemot (Uria aalge)	3	0.3	-	-
Black Guillemot (Cepphus grylle)	3	0.1	2	0.2
Puffin (Fratercula arctica)	2383	95.2	1054	98.4
Rock Pipit (Anthus spinoletta)	1	0.1	-	-
Chicks				
Fulmar	24	1.5	-	-
Great Black-Backed Gull (Larus marinus)	4	0.1	-	-
Kittiwake	3	0.1	-	-
Razorbill	66	1.0	31	1.1
Puffin	44	1.3	-	-
Other Food				
Field Mouse (Apodemus sylvaticus hirtensis)	1		-	
Soay Sheep (leg bone of lamb)	1		-	
Eggs (Fulmar)	Unquant.		Unquant.	
Crabs (Carcinus maenas, Cancer pagurus)	7		18	
Fish (Backbones of various spp.)	9		27	
Scavenged cooked bone	3		2	

of other fish remains was waste from trawlers. Fragments of Fulmar (Fulmar glacialis) eggs were found at most middens during May and June in both years, but the number of eggs taken could not be readily quantified.

The proportion of different species of prey found at middens varied between Dun and other islands of the St Kilda group (Table 1.4).

Table 1.4 Food remains at L. marinus middens on other islands of the St Kilda group

Island	Hirta	Hirta	Hirta	Soay	Boreray
Area	Ruival	Oiseval	Carn Mor	Cleit Village	Landing Rocks
Date	28.6.77	.6.77	9.7.78	12.7.77	13.7.77
Middens	3	1	1	4	2
Prey					
Adult birds					
Manx Shearwater	-	1	4	3	-
Leach's Petrel	-	-	-	3	-
Puffin	24	8	28	c.50	c.20
Turnstone	1	-	-	-	-
Chicks					
Herring gull	1	-	-	-	-
Other food					
Crab	20-30	10+	-	-	-
Fish bones	4	15+	-	-	-

Remains found at Carn Mor and Soay included more Manx Shearwater (Puffinus puffinus) corpses than the total found on Dun, and the majority of remains at Ruival and Oiseval on Hirta were Shore crab (Carcinus maenas) shells and fish bones.

Adult and recently fledged gulls were seen eating Goose Barnacles (Lepas sp.) from floating timber near Dun in August 1977. Barnacle remains were not found at middens, but by this time most gull chicks had fledged and many middens were no longer in regular use.

Discussion

Data on remains found at middens suggest that adult Puffins were the main source of food for gulls breeding on Dun, but these figures could be misleading if certain prey remains, such as fish bones and crab shells, were excreted away from middens and not found. Comparison of the contents of middens on Dun and other islands suggests that such omissions were unlikely to have biassed estimates of the proportion of non-avian prey in gull diet at different sites. If it assumed that gulls breeding on Hirta, within three kilometres of Dun, processed fish and crabs in the same way as Dun gulls, the large number of fish and crab remains found at Hirta middens suggests that such prey comprised a larger part of gull diet on Hirta than on Dun. Quantifying the amount of such prey eaten would require analyses of faecal samples and chick stomach contents. For the purposes of the present study such analyses were considered unnecessary, due to the striking visual differences between middens on Dun and other islands. Fish remains were rarely found at a Dun midden, whereas fish bones were common at Hirta middens.

Considering avian prey remains at Dun middens, data presented here suggest that gull predation on adults of species other than Puffin was casual rather than systematic. Such prey could have consisted of birds found sick or injured, since L. marinus, in common with many other avian predators, has been

widely recorded killing weak individuals of other species in an opportunistic fashion (Presnall 1968, Macdonald and Mason 1973). The possible exception is the killing of Black Guillemots (Cepphus grylle). This species suffered heavy predation relative to its population on Dun, the five corpses recovered at middens possibly representing as much as 25% of the Dun breeding population in the two years of study (Harris and Murray 1978). Black Guillemots in breeding plumage are strikingly marked with black and white feathers and bright red bills and perform noisy courtship displays in groups on the water (Asbirk 1979). The conspicuousness of this species may have made it an easy target for Dun gulls, but since it was present only in small numbers, an unsuitable source of food for supporting gulls throughout the breeding season.

1.4 PREY SELECTION BY GULLS AT OTHER LOCALITIES

Most accounts of prey selection by gulls at other localities are general descriptions of which avian prey are selected and how such prey are killed (e.g. Lowe 1913, Gross 1945, Davis 1958, Mylne 1960, Gordon 1965). There are also notes on gull predation of other vertebrates such as rats (Rattus rattus) (Harber and Johns 1947), on kleptoparasitism by gulls (Ingolfsson 1969, Prys-Jones 1973), and one study of the extent of egg predation by gulls in Arctic Tern colonies in Iceland (Cody 1964).

Aside from studies conducted on Skomer, North Rona and Copinsay there is little data on gull diet based on food remains found at other British breeding sites (Ainslie and Atkinson 1937, Harris 1965, Corkhill 1973, Love 1974, Evans

1975, Beaman 1978). The stomach contents of 41 gulls from unspecified sites in Britain were detailed by Collinge (1924 - 27).

Detailed studies of gull diet outside Britain, in Iceland and Murmansk, are also based on analyses of stomach contents (Belopolskii 1961, Ingolfsson 1967, 1976).

The species composition of avian prey at different sites varies considerably (Table 1.5). Although, as on Dun, Puffins comprised the bulk of avian prey selected by gulls on North Rona in different years, there was more predation on small petrels at this site than on Dun. In complete contrast to Dun, gulls on Skomer killed few Puffins relative to the large numbers of Manx Shearwaters taken at that site. On Grimsey, Iceland, young and adult Kittiwakes formed over 70% of remains found at middens during the present study, and more Guillemots were taken than on Dun (Table 1.6).

Comparison of the overall diet of gulls in Russia, Wales and on Dun indicates further differences in prey selection in these different areas (Table 1.7). Russian gulls fed primarily on fish and on other non-avian prey such as molluscs. Fish comprised over 20% of the diet of gulls on Skomer, and mammals (Rabbits (Oryctolagus cuniculus)) were also included in the diet to a much greater extent than on Dun. (The bulk of food in stomachs analysed by Collinge (1924 - 27) was fish and molluscs.)

In Iceland, Ingolfsson (1967, 1976) considered gulls to be rather generalist feeders, but primarily predators on birds and fish. This author felt that L. marinus was the least specialised feeder of the Larus gulls breeding in Iceland, and that it had an ability to exploit foods which suddenly became abundant, such as Eider (Somateria mollissima) ducklings.

Table 1.5. Species composition of L. marinus avian prey at different localities

Study area	North Rona	North Rona	North Rona	North Rona	Skomer	Dun	Dun
Date	Aug 1936	Jul 1971	Jun/Jul 1972	Jul 1972	Feb-Oct 1962	1977	1978*
Bird Remains	163	65	237	20	222	2536	1091
Birds as % Total Food	Not known	Not known	50%	Not known	53.1	99.2	95.9
Source	Ainslie and Atkinson 1937	Love 1974	Evans 1975	Evans 1975	Harris 1965	This study	
Prey							
Manx Shearwater	-	-	-	-	84.3	0.1	0.1
Small Petrels	6.8	16.9	17.7	-	-	0.1	0.2
Larus spp. juv.	4.9	-	22.4	-	7.2	0.1	-
Kittiwake ad.	22.1	3.1	6.3	5.0	0.5	0.1	-
Kittiwake juv.	16.0	33.9	2.5	-	-	-	-
Puffin ad.	49.1	46.2	32.9	75.0	2.2	94.0	96.6
Puffin juv.	-	-	-	-	2.2	1.7	-
Other birds ad.	1.2	-	2.5	10.0	1.8	0.4	0.3
Other birds juv.	-	-	15.6	10.0	1.8	3.5	2.8

*Data from midden clearances by K.Taylor 8 June to 8 July 1978.

Table 1.6. Contents of L.marinus middens, Grimsey, 2/8/79

Sp. / Midden	Kittiwake Ad.	Kittiwake Juv.	Com.Guill	Brun.Guill	Puffin	Razorbill Ad.	Razorbill Juv.	Fulmar Ad.	Fulmar Juv.
1	5	3	2	-	-	1	-	1	1
2	8	4	3	1	1	1	-	3	-
3	13	2	3	-	-	2	-	-	-
4	12	7	3	-	2	1	2	1	-
5	9	5	3	-	-	-	-	-	-
6	3	-	-	1	2	-	-	-	-
Total	60	21	14	2	5	5	2	5	1
%	52.2	18.3	12.2	1.7	4.4	4.4	1.7	4.4	0.9

Table 1.7. % contribution of different prey types to the diet of L. marinus in Russia and Britain

Study Area	Murman	Skomer	Dun
Date	1940's	1962	1977/78
Source	Belopolskii 1961	Harris 1965	This study
	% Contribution of prey type		
Birds	6.7	53.1	98.2
Fish	40.4	21.4	1.0
Mammals	0.2	15.7	0.1
Refuse	0.6	6.7	0.1
Other	52.1	3.2	0.6

Opportunistic feeding is also suggested by various accounts of gulls selecting unusual or injured prey (e.g. Gleghorn 1942, Addy 1945, Tinbergen 1953); or prey which are only available for part of the year, such as Little Auks (Plautus alle) wintering in Britain (Paterson 1895); or coping with local conditions in selecting prey, such as gulls on Nesøya in Norway which took domestic chickens from coops (Mehl, 1957).

It has been suggested for some other British colonies that adult seabirds are mainly selected as prey by specialist pairs of gulls, rather than all gulls breeding in a locality taking a few such prey. Only about 50 of the 200 or so pairs of gulls breeding on the Shiant Islands were considered by Brooke to be responsible for the Puffin kill observed there (Brooke 1972). Evans, writing of North Rona, felt that 'only one or two individuals at the colony' (of c.2,000 pairs) 'were preying on Puffins, the bulk of the population appearing not to be interested' (Evans 1975). Variations in the number of seabirds killed by different gull pairs were also noted on Skomer, where some pairs ate 'few if any' Manx Shearwaters (Harris 1965), and on Copinsay, where solitary nesting pairs had a higher proportion of seabirds in their diet than colonial birds (Beaman 1978).

Discussion

Information presented above indicates that gulls exploit a wide variety of vertebrate and invertebrate prey at different localities, and that the extent to which they specialise, if at all, on one or a few prey species varies considerably from place to place. Differences in prey selection on Dun, Skomer and Grimsey suggest that differences in the relative

abundance of different prey species may account for some of the variation in gull diet between different localities. At each of these sites, the bulk of gull prey consisted of the most numerous seabird species breeding there. Other species of bird were seldom killed, or on Grimsey, taken in quantities proportionate to the relative breeding abundance of the different species near gull nests. Selection of the most abundant species of prey in a locality may give gulls a higher energy return against energy expended hunting, and this aspect of gull behaviour is discussed at length in relation to theories of optimal foraging in Chapter Three.

Fish were more widely present in the diet of gulls elsewhere than on Dun. It has already been shown that the midden clearance technique used to assess gull diet on Dun was unlikely to have seriously under-recorded fish prey selected by gulls there. Some differences in the amount of fish recorded in gull diet at other localities may have been because data came from stomach analyses rather than quantification of food remains at middens. Comparison of the diet of gulls at sites where data was collected by inspecting middens, such as Skomer, North Rona and Grimsey, suggests that lack of stomach content data for Dun gulls does not seriously bias comparison of the diet of Dun gulls with the diet of gulls elsewhere.

Differences in the nesting dispersion of gulls breeding at high density on North Rona and colonially on Copinsay compared with the solitary nesting habits of most Dun gulls, suggest real differences in the feeding behaviour of gulls at the former two sites compared with those on Dun. As has been suggested earlier, colonial breeding might be favoured by individuals exploiting a patchy, unpredictable food source

such as the Sandeels (Ammodytes marinus) selected by colonially breeding gulls on Copinsay, but not by individuals exploiting a predictably abundant food source, such as the Puffins eaten by Dun gulls.

In conclusion, Dun gulls in 1977 and 1978 showed a more extreme degree of food specialisation than has been recorded for the species at sites elsewhere. Given the importance of adult Puffins to Dun gulls, did gulls which caught fewest Puffins raise less young than gulls which caught more Puffins; and was there evidence from the temporal and spatial pattern of gull predation on Puffins and other species that gulls hunted their prey in feeding areas near their own nests? Data in the rest of this chapter examine these questions.

1.5 VARIATIONS IN THE NUMBER OF PUFFINS FOUND AT MIDDENS IN RELATION TO GULL BREEDING CHRONOLOGY AND BREEDING SUCCESS

Information on annual totals of Puffins killed by Dun gulls has already been published by Harris (1980). Data presented in this section extends this information by documenting changes in the number of Puffins killed during the gull breeding season and the extent of Puffin killing by different pairs of gulls. These and other data are used to assess whether gull breeding performance was related to differences in Puffin breeding density near nests in Sparse and Dense areas, and whether gulls which caught fewest Puffins raised fewest young.

Results

Changes in Puffin killing during the gull breeding season

The spread of hatching for 26 clutches whose hatching date

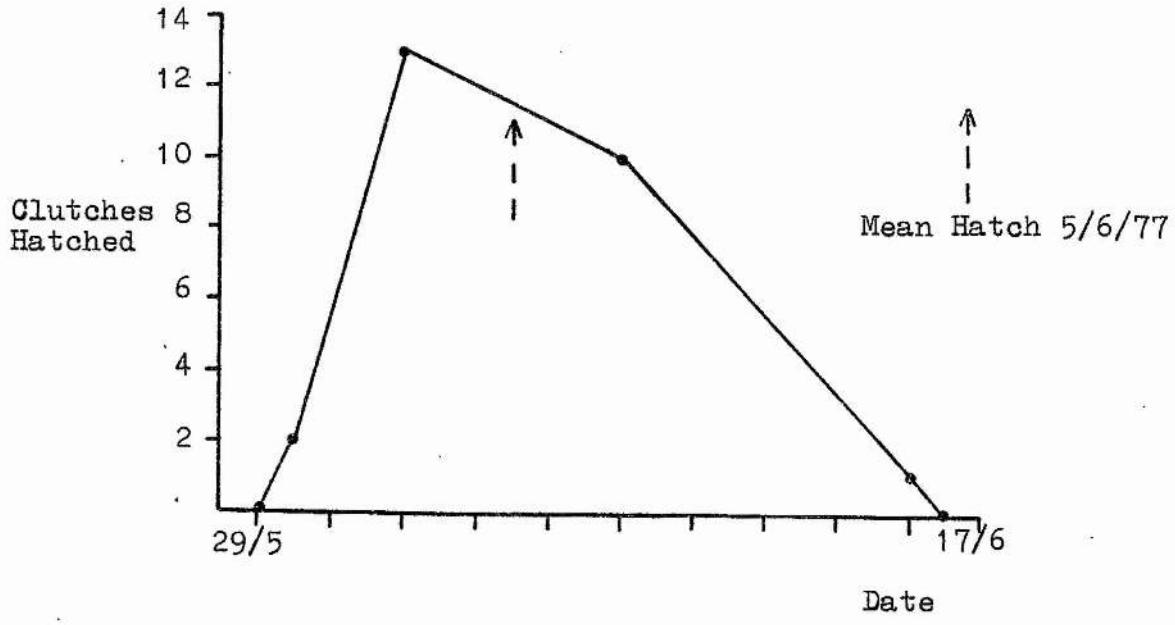


Fig. 1.5. Spread of hatching in 26 gull nests with known hatch date in 1977

was known to within seven days in 1977 is illustrated in Fig. 1.5. Mean hatch date was 5 June in both 1977 and 1978, with chicks fledging in late July and early August.

More Puffins were killed by gulls during the nestling period than at other times (Fig. 1.6). Gulls which failed in a breeding attempt brought few, if any, Puffins or other prey to middens after the loss of eggs or chicks, as illustrated by the cumulative number of Puffin corpses found at middens used by gulls from nests 7 and 25 in 1977 (Fig. 1.7).

The mean total of Puffins found at eight middens, each used by just one pair of gulls which successfully fledged chicks in 1977, was 138 ($\pm$ 12) for 87 days of study from 15 May. Assuming that Puffins found at middens on 15 May had been killed during May, 138 Puffins would have been killed in 101 days, an average of 1.37 per pair per day throughout the breeding season. Differences in the frequency and extent of midden clearances between 1977 and 1978 do not allow a similar calculation to be made for single pairs for the whole of the 1978 breeding season. However, for seven middens, each used by just one pair of gulls known to be feeding young in June 1977 and 1978 and cleared by myself in both years, there was no significant difference in the number of Puffins found in the two years (Wilcoxon T = 5, N = 7 matched pairs, $P > 0.05$) (Table 1.8).

The number of adult Puffins found at middens fell drastically during the latter part of the nestling period, as illustrated in Fig. 1.7 and by data on the number of Puffins killed per day after 15 May by two pairs which fledged chicks in 1977 (Fig. 1.8).

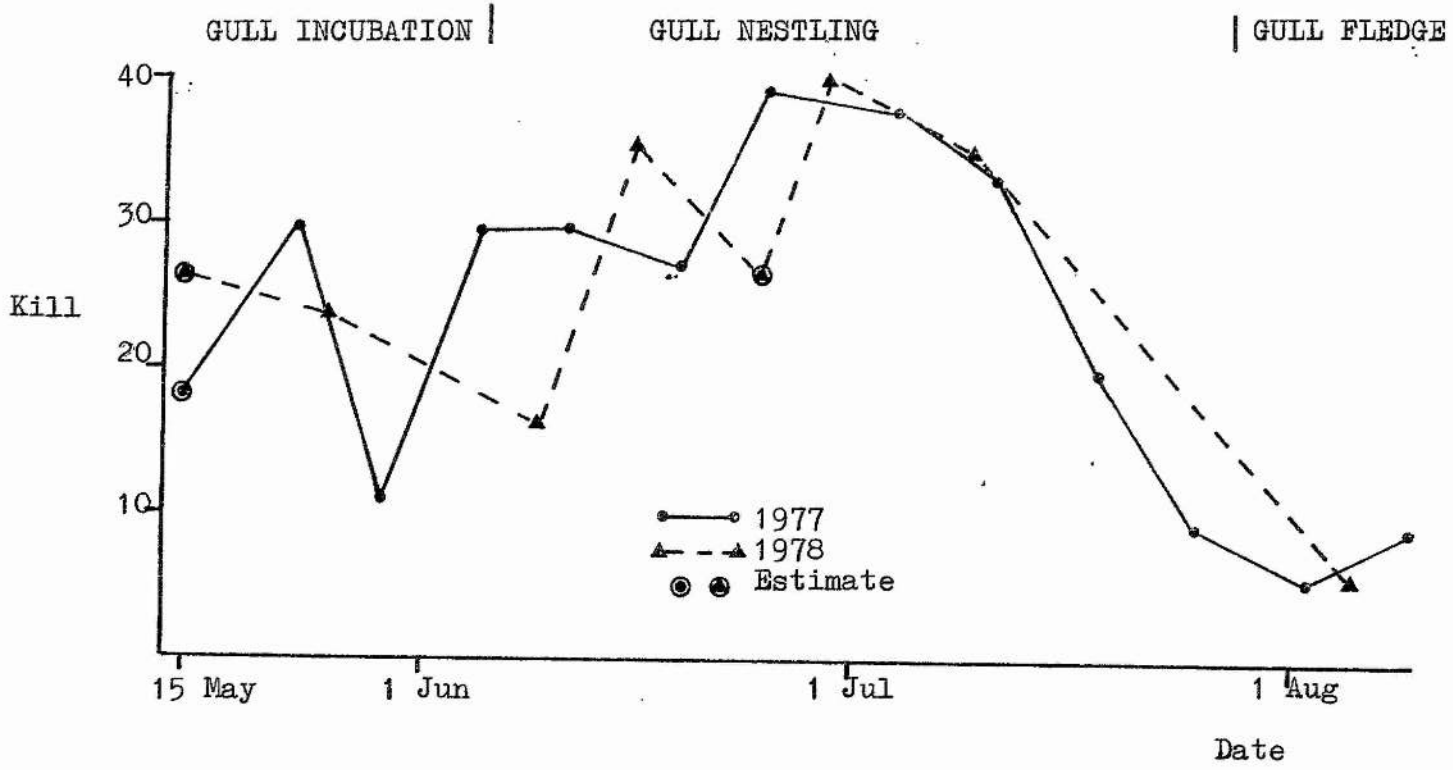


Fig. 1.6. Total Puffins (adults) killed per day and gull breeding chronology

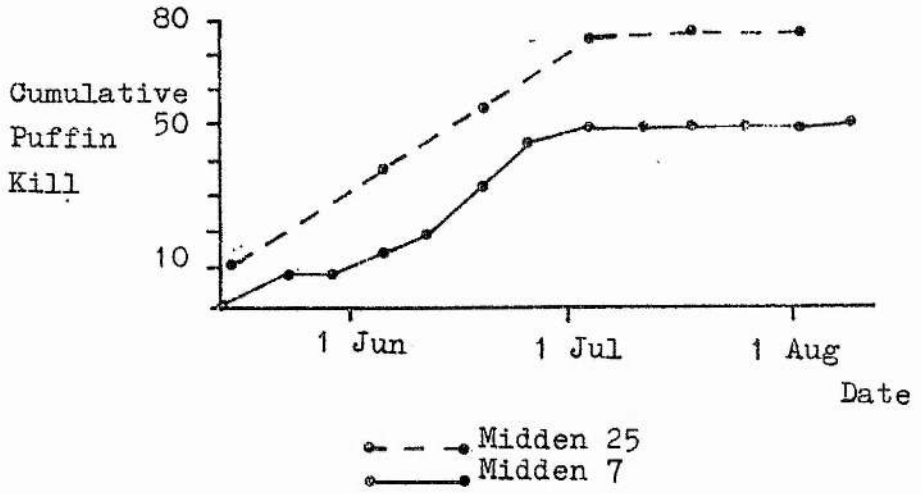


Fig. 1.7. Cumulative Puffin kill at middens of gull pairs which failed in breeding attempt during nestling period in 1977

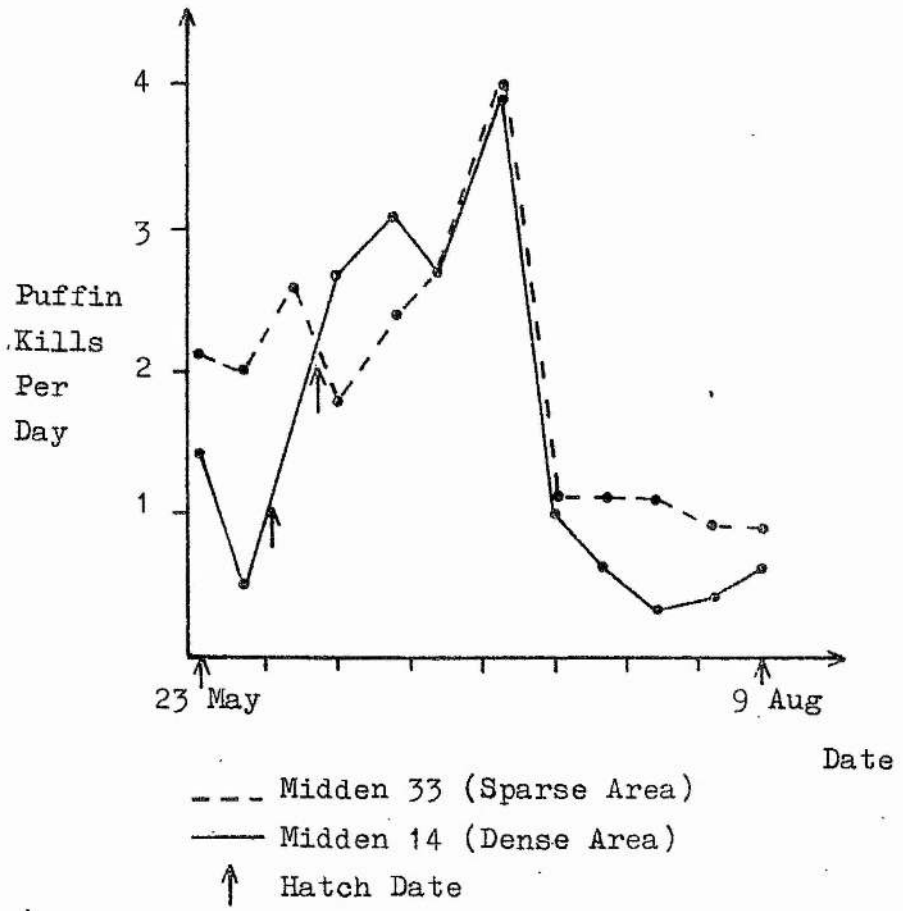


Fig. 1.8. Puffin kills at middens, May to August 1977

Table 1.8. Puffin kill in June at middens of L. marinus pairs with chicks, 1977 and 1978

Midden	1977 Total	Per Day	1978 Total	Per Day
8	64	2.1	71	2.4
12	67	2.2	55	1.8
14	68	2.3	70	2.3
15	70	2.3	24	0.8
16	48	1.6	43	1.4
25	37	1.2	33	1.1
33	64	2.1	49	1.6
Mean	59.7±4.7	2.0±0.1	49.3±6.7	1.6±0.2

No difference between kills at the same middens between years (Wilcoxon T = 5, 7 matched pairs, $p > 0.05$).

Gull breeding success in Sparse and Dense areas

More than a third of all gulls nesting on Dun failed to raise young in 1977 and 1978 and there was no significant difference in the proportion of failures in the two years (Table 1.9a). In 1977, a significantly higher proportion of gulls nesting in the Sparse area failed to raise young than gulls nesting in the Dense area (Table 1.9b). There was no such difference in the relative breeding performance of gulls nesting in these areas in 1978 (Table 1.9c). Pairs nesting in the Sparse area had smaller clutches than pairs nesting in the Dense area in both years (Table 1.10).

Hatching success of eggs in the Sparse area was 42.2% in 1977, significantly lower than the 69.4% hatching success of eggs in the Dense area ($\chi^2 = 7.12$, $P < 0.005$, $n = 81$ eggs). In 1978, 61.5% of Sparse area eggs hatched, similar to the 65.2% hatch success of Dense area eggs in that year.

In 1977, 47.4% of 19 chicks hatched in the Sparse area fledged, not significantly different from the 63% fledging success of 27 chicks hatched in the Dense area. In 1978 fledging success of chicks hatched in these areas was again similar, with 78.6% of 14 Sparse area chicks monitored after hatching fledging and 76.9% of 13 Dense area chicks fledging.

1.6 THE NUMBER OF PUFFINS KILLED AND GULL BREEDING SUCCESS

In both 1977 and 1978 fewer Puffins were found during the incubation period at middens of pairs which failed to hatch chicks than at middens of pairs which did hatch chicks (Mann-Whitney $U = 0$, $P < 0.001$ both years) (Table 1.11). On average, pairs which did hatch chicks caught one to two Puffins

Table 1.9. Breeding success of L. marinus on Dun

a. Whole island, both years of study

Year / Nest Fate	1977	1978	
Known Success	18	16	34
Known Fail	17	10	27
	35	26	61

No difference in the proportion of successful nests on the whole island between years, (χ^2 = 1.10, N.S.).

b. Sparse and Dense Areas, 1977

Area / Nest Fate	Sparse	Dense	
Known Success	7	11	18
Known Fail	13	4	17
	20	15	35

More failures in the Sparse Area than in the Dense Area in 1977 (Fisher Exact p = 0.028).

c. Sparse and Dense Areas, 1978

Area / Nest Fate	Sparse	Dense	
Known Success	9	7	16
Known Fail	5	5	10
	14	12	26

No difference in sub-area success in 1978 (χ^2 = 0.01, N.S.).

Table 1.10. Clutch size of gulls nesting in Sparse and Dense colony areas

	1977		1978	
	Sparse	Dense	Sparse	Dense
Mean clutch	2.24±0.63	2.73±0.03	2.5±0.14	3.0±0
Known final clutch nests	21	15	14	11
Mann-Whitney U	92		38.5	
P	<0.0001		<0.005	

Table 1.11. Puffins killed per day during incubation period and gull hatching success

	15/5 to 5/6/77		15/5 to 8/6/78	
	Hatched chicks	No Hatch	Hatched chicks	No Hatch
Pairs monitored	8	5	5	7
Mean kill per day	1.75±0.17	0.50±0.09	1.48±0.25	0.38±0.07
Mann-Whitney U	0		0	
P	<0.001		<0.001	

Table 1.12. Re-occupation of L.marinus nest sites on Dun in 1978 in relation to breeding success at these sites in 1977.

1977 Performance / 1978 Occupation	Fail	Success	
Abandoned	5	2	7
Re-occupied	7	21	28
	12	23	35

Failure sites significantly more likely to be abandoned in the following breeding season (Fisher Exact p = 0.03).

per day during the incubation period in both years, whereas pairs which failed to hatch eggs caught only one Puffin per two days or longer. There was no significant difference in either year between Sparse and Dense areas in the number of Puffins killed per day by pairs which failed to hatch eggs and no significant difference between the two areas in the Puffin kill per day of pairs which did hatch chicks (Mann Whitney $U_p > 0.05$ all comparisons). Significantly fewer nest sites of pairs which did not raise chicks in 1977 were re-occupied in 1978 than nest sites of pairs which did raise chicks (Fisher exact $P = 0.0298$, $n = 35$ nest sites) (Table 1.12).

Discussion

Previous reports of L. marinus egg production range from 2.67 to 3.00 eggs per pair, with hatching success ranging from 39 to 95% (Harris 1964, Erwin 1971, McGill 1977, Burger 1978, Møller 1978, Verbeek 1979, Butler and Tivelpiece 1981). Egg production of Sparse area pairs was thus lower in both years of study than previously recorded at sites elsewhere, and Sparse area hatching success in 1977 was also lower than recorded at most other colonies. In contrast, Dense area egg production and hatching success was similar to that of gulls in many other colonies.

Low hatching success among gulls on Rhode Island was attributed to excessive defence of territories against Herring Gulls breeding near L. marinus nests (Erwin 1971). On Little Duck Island, Maine, gulls breeding in high nest density areas fledged fewer chicks than gulls in low density areas, and engaged in more agonistic interactions and chick oriented

vocalisations (Butler and Tivelpiece 1981). Nests in the Rhode Island and Little Duck Island studies were much closer together than nests on Dun; (for example, the mean nearest neighbour distance of 'low' density Little Duck Island nests was 12.1 m., in comparison to the minimum mean distance of 47.9 m. observed on Dun in the present study). Some factors influencing gull breeding success at these sites may thus not have been important for gulls on Dun. For example, there could have been a higher risk of chicks wandering into neighbouring territories and being attacked by adult gulls at Rhode Island and Little Duck Island than on Dun (cf. Hunt and McCloon 1975).

There is no detailed information in previous reports of L. marinus breeding success quantifying whether food supply influenced the breeding success of individual pairs, although Burger (1978) suggested that abundant food may have contributed to high breeding success of gulls breeding in New Jersey. On Dun, most breeding failures occurred during the incubation period. At this time, failure to hatch chicks was associated with low numbers of Puffins at middens of unsuccessful pairs, whereas pairs which did hatch chicks caught greater numbers of Puffins at all stages of the breeding season. This difference could have arisen if gulls caught Puffins in hunting territories which were defended against other gulls, and, as a result of such behaviour, some gulls were unable to gain adequate access to Puffin prey to meet the energy requirements of breeding.

Inadequate access to Puffin prey could have made a breeding attempt costly, due to the expenditure of energy in competing with gulls which held hunting territories, or in flying

to and from Dun searching for other prey. (For example, one member of pair 7 in the Sparse area died of starvation towards the end of the incubation period in 1977.)

Poor breeding success of Sparse area pairs relative to Dense area pairs in 1977 could have been due in part to the the high density of nests there in that year. However, the low clutch size of Sparse area pairs suggests that the density of Puffin prey may also have influenced breeding performance. If Sparse area birds needed to expend more energy in hunting Puffin prey than Dense area pairs, this could have resulted in Sparse area females having less energy available for egg production than Dense area females. Such extra energy expenditure could have arisen if, for example, Sparse area gulls required to range farther and spend more time hunting Puffin prey at low densities than Dense area gulls which had ready access to high density prey. Recoveries of Puffins ringed on Dun and later found at middens provide evidence that Sparse area gulls did range farther from their nests to catch Puffins than Dense area gulls (Harris 1980).

That the number of eggs laid by birds may be related to the energy available to the parents for raising chicks was first suggested by Lack (1954). Lack hypothesised that birds produce that number of eggs which results in the maximum number of young surviving to reproduce, and data are now available from many field studies which support this hypothesis (summarised in Emlen 1973). In particular, there is evidence that some species of bird with a highly variable food supply vary clutch size in response to changes in food abundance, laying large clutches in good food years and small clutches in poor food years (Lack 1968). For example, the Swift

(Apus apus) lays three eggs in years when insects are abundant, but only two when insects are scarce (Koskimies 1950). There is evidence from studies of tits that competition for food may influence egg production. Great tits (Parus major) and Yellowhammers (Emberiza citrinella) lay smaller clutches in years when there are larger numbers of breeding pairs than when the breeding density is low (Perrins 1979, O'Connor 1980).

For gulls on Dun, the low density of Puffin prey in the Sparse area may influence clutch size of Sparse area gulls, leading to smaller clutches than in the Dense area. In a year when many gulls nest in the Sparse area, such as 1977, competition for prey could further reduce the food available to female gulls early in the breeding season, and further depress egg production relative to female gulls in the Dense area.

1.7 VARIATIONS IN THE AGE-CLASS COMPOSITION OF PUFFINS KILLED BY GULLS

Seasonal attendance of immature Puffins at the breeding colony has been documented by Harris (in press). Few first year Puffins come ashore, but older Puffins return progressively earlier to the colony with increasing age from two years old. An influx of immatures occurs later in the incubation period, usually around the middle of May at British colonies.

Gulls on Dun killed more Puffins during the gull nestling period than at other times. Since a greater range of Puffin age-classes was available as prey at this period than earlier in the breeding season, what proportion of the Puffin kill

consisted of immature birds, and did gull pairs differ in the extent to which they selected immature Puffins as prey? Data presented in this section document the age-class composition of Puffin prey found at different middens throughout the breeding season to examine these questions. These data indicate whether there were seasonal and geographical differences in the risk of predation to adult Puffins on Dun. Throughout this section 'immature' means a Puffin with less than two bill grooves, as described earlier.

Results

The remains of immature Puffins were found at middens on every clearance from the last week in May onwards in both 1977 and 1978. Corpses of Puffins with less than one bill groove were found only in July and August (Fig 1.9). The main arrival of immature Puffins on Dun was on 24 May in 1977, as judged by observations of mass flight of Puffins around Village Bay and the occupation of rocks on Dun known from previous years to be used as loafing areas by immatures.

In 1977, immature Puffins formed a significantly greater percentage of the Puffin kill as the breeding season progressed, comprising 50% of all Puffin corpses found at middens on the last clearance in early August ($r_s = 0.98$, $P < 0.005$) (Fig.1.10).

In 1978, immature Puffins formed a smaller percentage of the Puffin kill than in 1977, and the number of immatures found at middens did not increase significantly between the gull incubation and fledging period ($r_s = 0.4$, $P > 0.05$)(Fig. 1.11). In that year, immatures comprised less than 20% of the Puffin kill from late June onwards, compared with the 22 to 50 percent recorded in the same period in 1977. Fluctua-

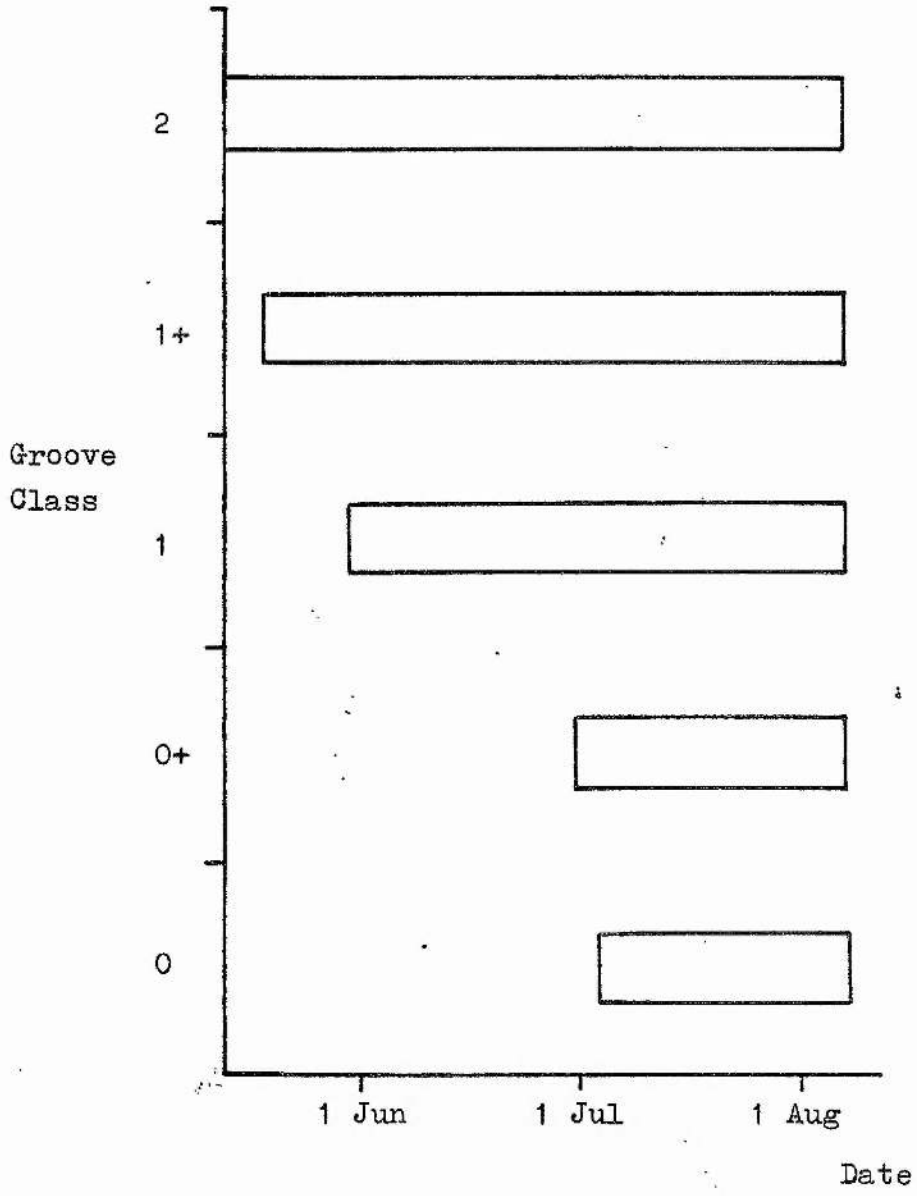


Fig. 1.9. Presence of different bill groove class Puffins in gull kill May to August. Data from 1977 and 1978 pooled

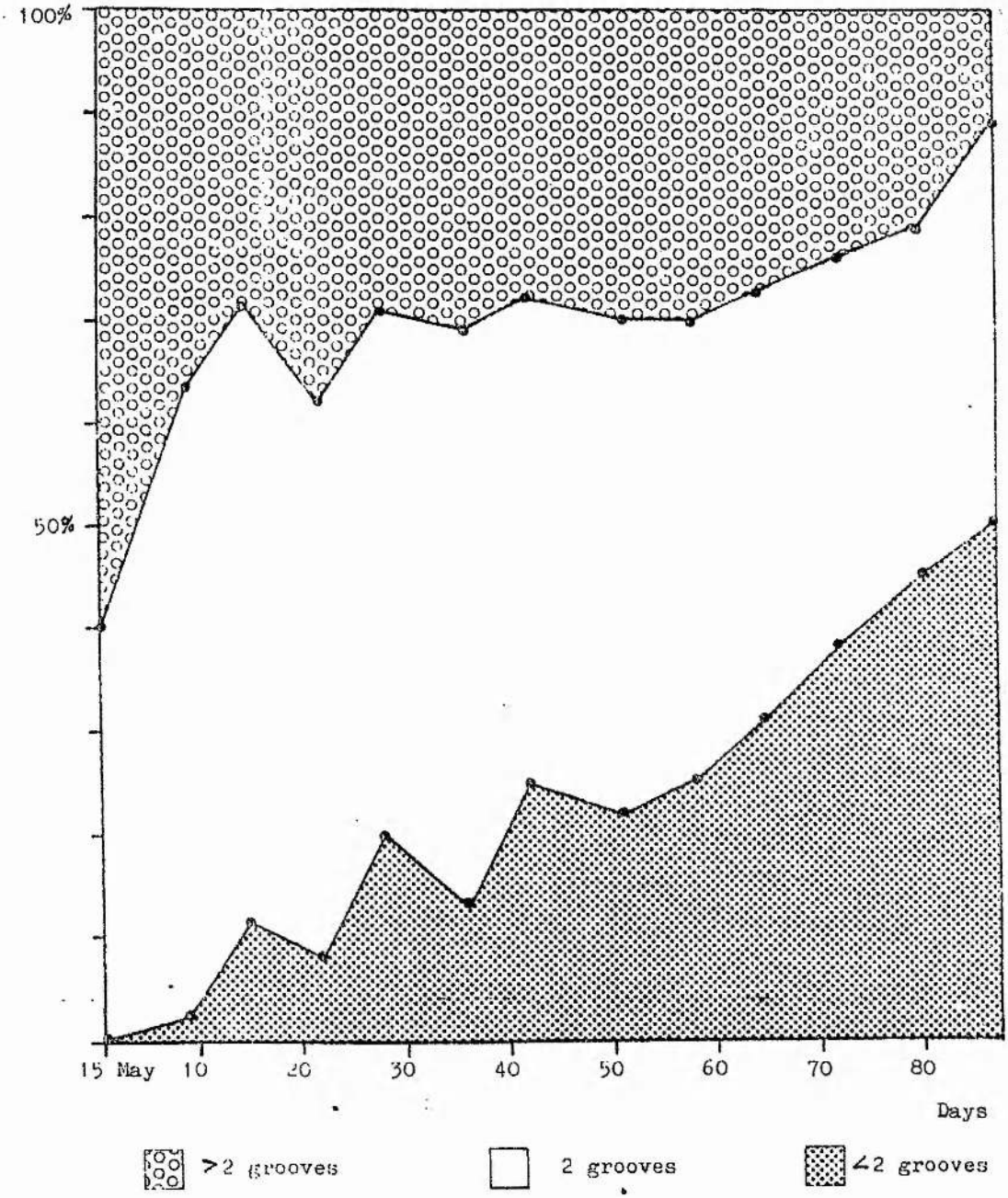


Fig. 1.10 % contribution of different bill groove classes to total billed Puffin kill, May to August 1977

(N=1728 billed corpses)

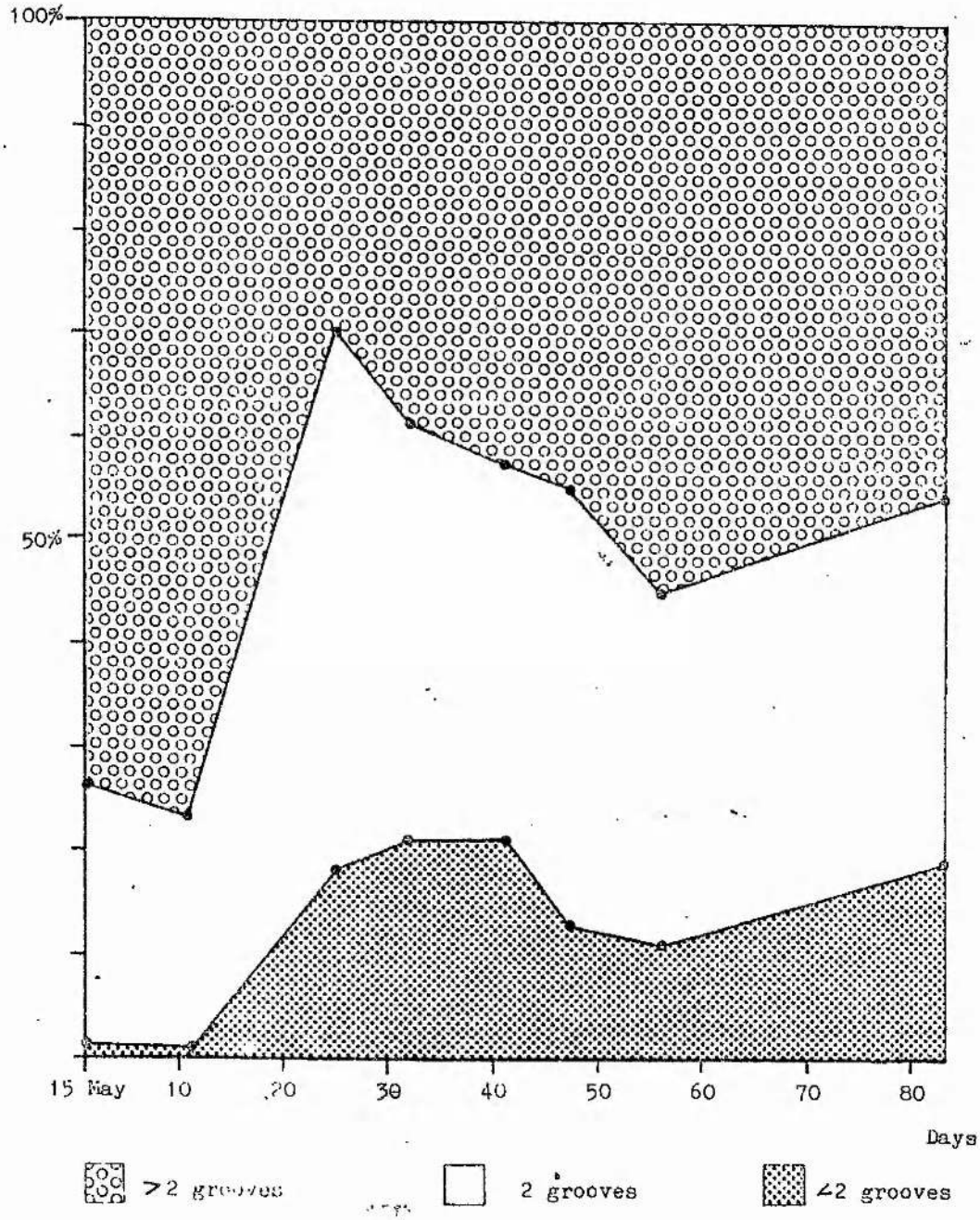


Fig. 1.11 % contribution of different bill groove classes to total billed Puffin kill, May to August 1978
(N=1512 billed corpses)

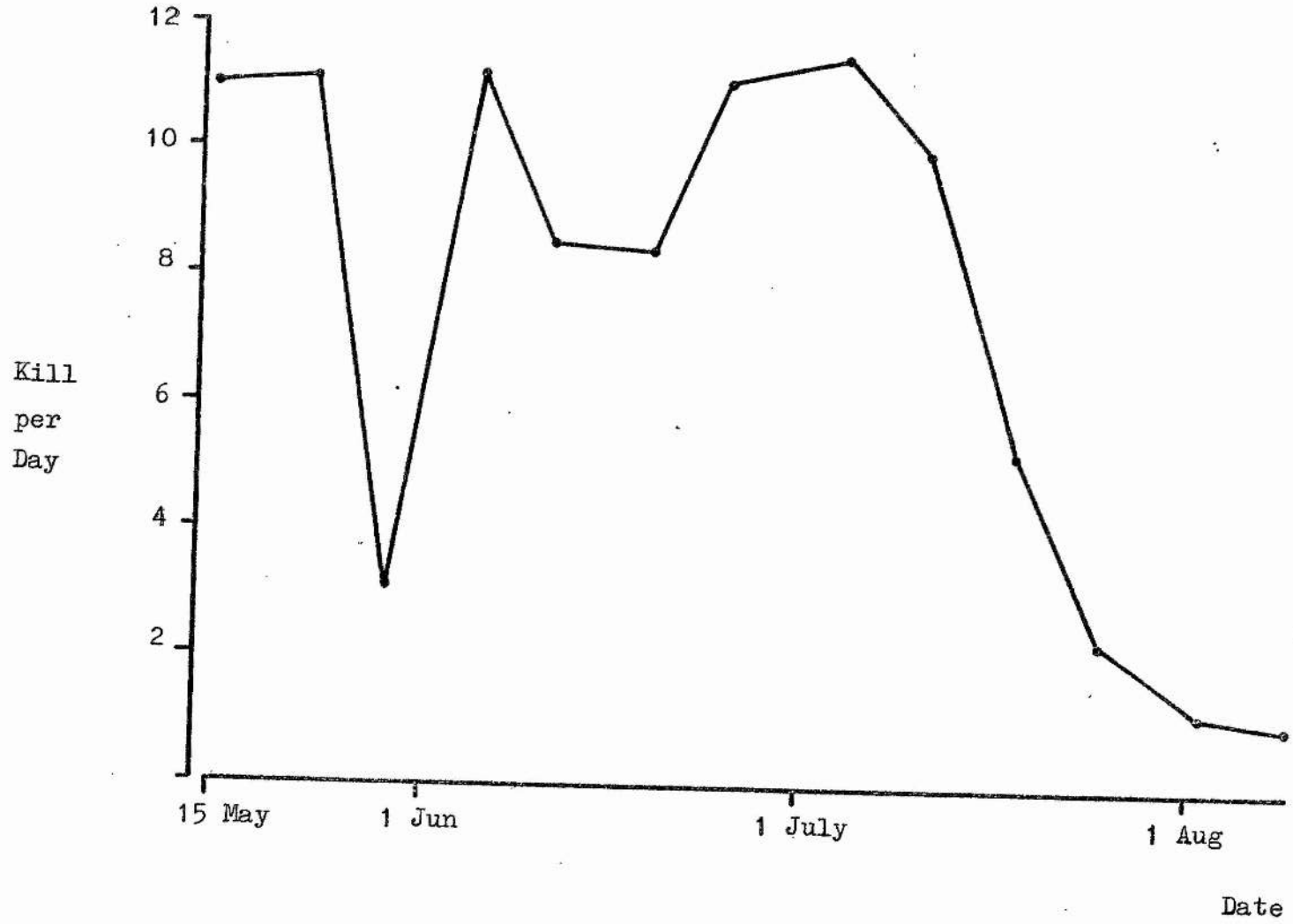


Fig. 1.12 Adult Puffins (2 grooves) killed per day, May to August 1977

tions in the number of immatures killed meant that an adult Puffin's risk of being killed by a gull was not constant throughout the breeding season, as illustrated for the period 15 May to 9 August 1977 (Fig. 1.12).

The age-class composition of Puffins found at different areas of Dun

In 1977 midden 17 in the Dense area and midden 33 in the Sparse area contained over 27% of all immature corpses found on the island. The proportion of immatures to adult Puffins at midden 33 was significantly higher than at other Sparse area middens in both 1977 and 1978 (Table 1.13a). Midden 17 also contained relatively more immatures than other Dense area middens in 1977, but in 1978 the pair from nest 17 using this midden failed to hatch eggs and no Puffin remains were found at the midden after the incubation period (Table 1.13b). The proportion of immatures in the kill at midden 33 was similar in both 1977 and 1978 (χ^2 = 0.02, NS, N = 263).

In 1977, middens in the rest of the Sparse area (i.e. excluding midden 33) contained a significantly greater proportion of immatures than middens in the rest of the Dense area (i.e. excluding midden 17), but this was not the case in 1978 (Table 1.13c). The Puffin kill at Sparse area middens other than midden 33 contained a significantly smaller proportion of immatures in 1978 than in 1977 (χ^2 = 4.76, $P < 0.025$, N = 1096). Dense area middens other than midden 17 contained a similar proportion of immatures in both years (χ^2 = 0.12, NS, N = 1611).

In both years, immatures formed a significantly larger proportion of Puffins found at Dense area middens than the

Table 1.13. Immature Puffins in L.marinus kills, 1977 and 1978

a. An Fhaing

	1977 An Fh.	1977 Sparse		1978 An Fh.	1978 Sparse		1977	1978	
Imm.	61	100	161	20	47	67	61	20	81
Breeder	134	409	533	48	277	325	134	48	182
	195	509	704	68	324	392	195	68	263
		10.36			7.79			0.02	
P		***			***			NS	

b. Fort

	1977 Fort	1977 Dense	
Imm.	44	119	163
Breeder	85	657	742
	129	776	905
		25.14	
P		***	

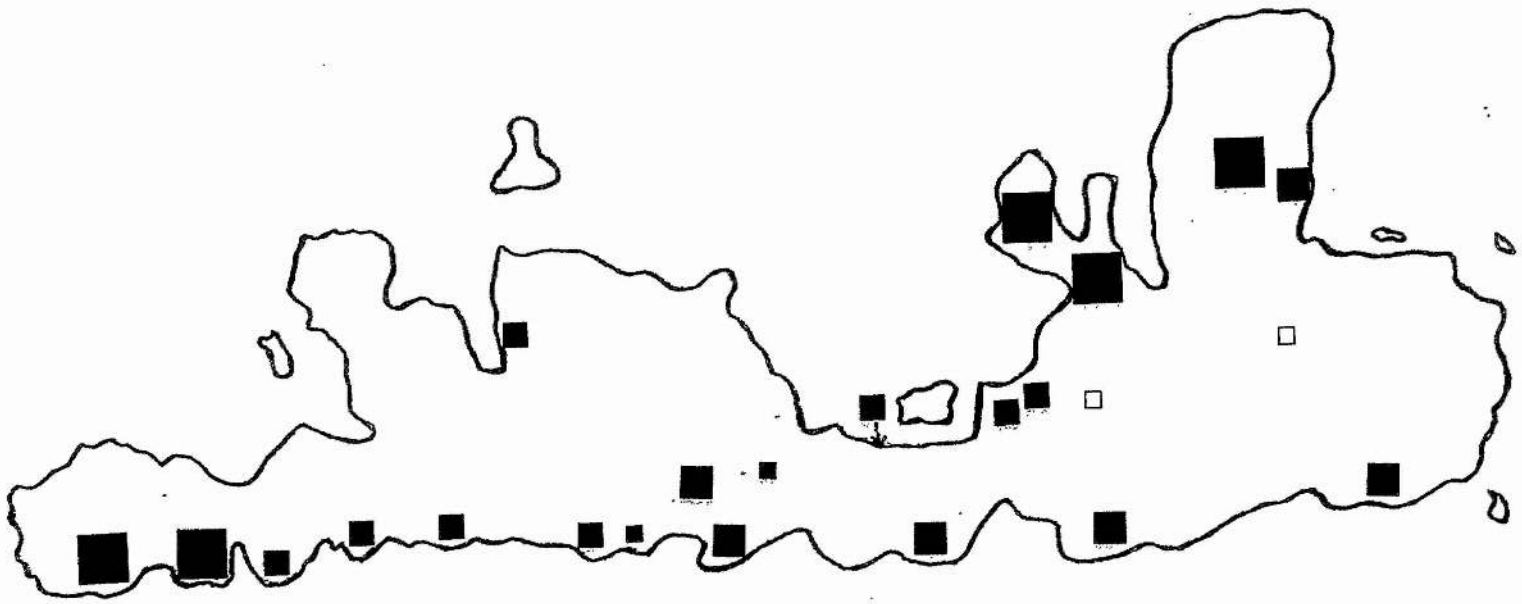
c. Rest of Sparse and Dense Areas

	1977 Sparse	1977 Dense		1978 Sparse	1978 Dense	
Imm.	100	119	219	67	131	198
Breeder	409	657	1066	325	575	900
	509	776	1285	706	392	1098
		3.74			0.47	
P		*			NS	

d. Dense Area kill and Dense Area mist-net catch

	1977 Kill	1977 Net	
Imm.	163	71	234
Breeder	742	773	1515
	905	844	1749
		33.9	
P		***	

(* P<0.05;*** P<0.005)



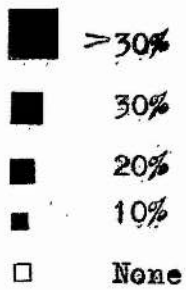


Fig. 1.13 Non-breeders (<2 grooves) in Gull kills 1977

proportion of immatures in a sample of Puffins mist-netted in the Dense area by M.P. Harris in July (Table 1.13d). Fewer than 10% of these mist-netted Puffins were immature, in contrast to the percentage of immatures found in the Puffin kill at the majority of middens, and strikingly different from middens in the Fort and An Fhaing areas (Fig. 1.13).

Discussion

The temporal pattern of predation on immature Puffins on Dun, with the youngest birds with less than one bill groove being caught only late in the breeding season, agrees well with data from other colonies on the seasonal pattern of attendance by immatures of different ages (Harris in press). This does not explain why gulls caught more immatures than would be expected from mist-net catches, and why gulls in some areas of Dun, noteably at An Fhaing and the Fort, caught many more immatures than gulls in other areas.

During the Puffin nestling period adult Puffins spend most of the day flying to and from fishing grounds to provision their chicks. Adult Puffins do join wheeling flocks of Puffins flying around the colony, but birds with fish spend less time wheeling before landing at the colony than birds without fish (this study, Chapter Three). In contrast, immature Puffins spend much of their time during the nestling period loafing on rocks or grass hummocks, interacting with other immatures and adults, flying in wheel flocks and prospecting for nest burrows (Taylor 1976, Hudson 1979). Some areas of Dun were used more than others by loafing birds. This was the case at the Fort, which consists mainly of large boulder blocks, and at a number of sites

immediately west of An Fhaing. (No Puffins bred on the lower part of An Fhaing itself.) Loafing Puffins were frequently seen in these areas during periods when there were few or no other Puffins loafing in other parts of the island. The spatial pattern of immature Puffin kills, with most immatures being found at the Fort, An Fhaing and west of An Fhaing, thus reflected the actual distribution and local abundance of immature Puffins on Dun. The greater availability of immature Puffins around gull nest sites near An Fhaing than near sites outwith the Fort in the Dense area could account for the greater proportion of immatures in Sparse area middens than in Dense area middens in 1977.

Mist-nets were placed along the slopes of Dun to catch Puffins, rather than down the slopes. Puffins caught in the nets would thus generally have been birds flying in to or out from the colony, rather than birds in wheels which flew parallel to the nets along the slopes. Due to the positioning of nets, and due to disturbance caused by manning the nets (Puffins did not generally loaf near nets while ringing was in progress), the mist-net sample could thus have been biassed towards adult birds flying to and from burrows. Data on the percentage contribution of immatures to the kills of Dun gulls thus does not necessarily indicate that gulls preferentially selected immatures as prey. Rather, the temporal pattern of predation on immatures, and geographical differences in the extent of this predation, suggest that the proportion of immatures in the kills of different gulls was a reflection of the number of immatures available at different times and at different sites. This provides further evidence for the suggestion, made earlier on the basis of gull nest distribution and breed-

ing success data, that gulls caught Puffins in areas near their own nests.

If gulls did select prey at random from the Puffin population near their nests, differences in the percentage of immatures in the 1978 Puffin kill relative to the 1977 kill indicate that fewer immatures were present in 1978 than in the previous year. There is no published data on year to year changes in immature attendance available for any Puffin colony. The data presented here indicate that investigation of whether such changes do occur could be an interesting area for future research. In particular, detailed field observations of the proportion of immatures to adult Puffins seen in different years in part of a Puffin colony, and further monitoring of Puffin kills on Dun, could illuminate this hitherto neglected area of Puffin social behaviour.

1.8 THE EXTENT OF GULL PREDATION ON CHICKS OF THE PUFFIN AND OTHER SPECIES

It has been suggested that gulls could have been responsible for a heavy mortality of Puffin chicks on St Kilda in the past and that gull predation on fledging Razorbill and Guillemot chicks may have a detrimental effect on breeding stocks of these species at some colonies elsewhere (Williamson 1958, Tuck and Heinzel 1978). Data presented here indicate what proportion of gull diet comprised seabird chicks at different stages of the breeding season. This allows estimation of the proportion of Puffin chicks produced in the Sparse and Dense areas which fell prey to gulls, and suggests the extent of gull predation on the chicks of other species.

Methods

Most data are from midden clearances made in 1977. These clearances covered the entire Razorbill fledging period and most of the Puffin fledging period. Figures for the expected fledgeling production on Dun in 1977 are taken from data on the productivity of samples of burrows in Sparse and Dense areas monitored by Harris and Murray in that year (Harris and Murray 1977). Razorbill population figures are from Harris and Murray (1978) and Razorbill chick production estimated from data in Lloyd (1976).

Results

Few chicks were found at middens before early July, but chicks accounted for an increasingly higher percentage of food items and food biomass at middens from then until late July, when over 40% of all bird remains were chicks (Fig. 1.14). Most chicks killed were fledgeling Razorbills (66 found) and fledgeling Puffins (44 found), with smaller numbers of Fulmar, Kittiwake and L. marinus chicks.

Remains of 44 Puffin fledgelings were found between 26 July and 9 August 1977, 29 of these fledgelings having been killed between 26 July and 2 August (Fig. 1.15). This was the time of peak Puffin fledging on Dun.

Less than one percent of the estimated fledgeling production was killed by gulls in both Sparse and Dense areas. A higher proportion of Puffins fledging in the Sparse area was killed by gulls than Puffins fledging in the Dense area (Table 1.14). Middens 10, 11, 12 and 15 contained 48% of all Puffin fledgeling remains. These middens were sited close to the highest density Puffin breeding areas on Dun.

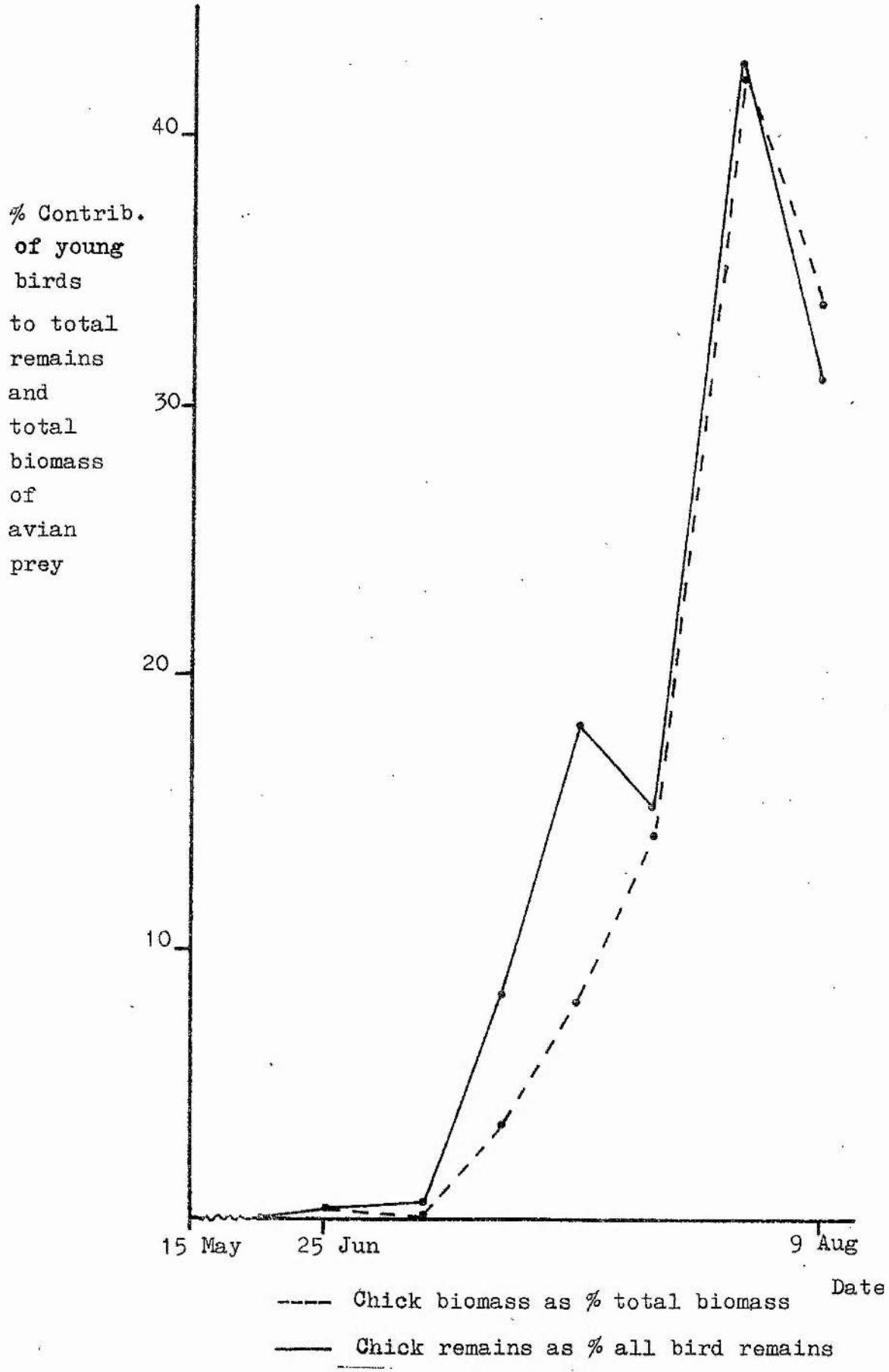


Fig. 1.14 % contribution of young birds to gull diet in 1977

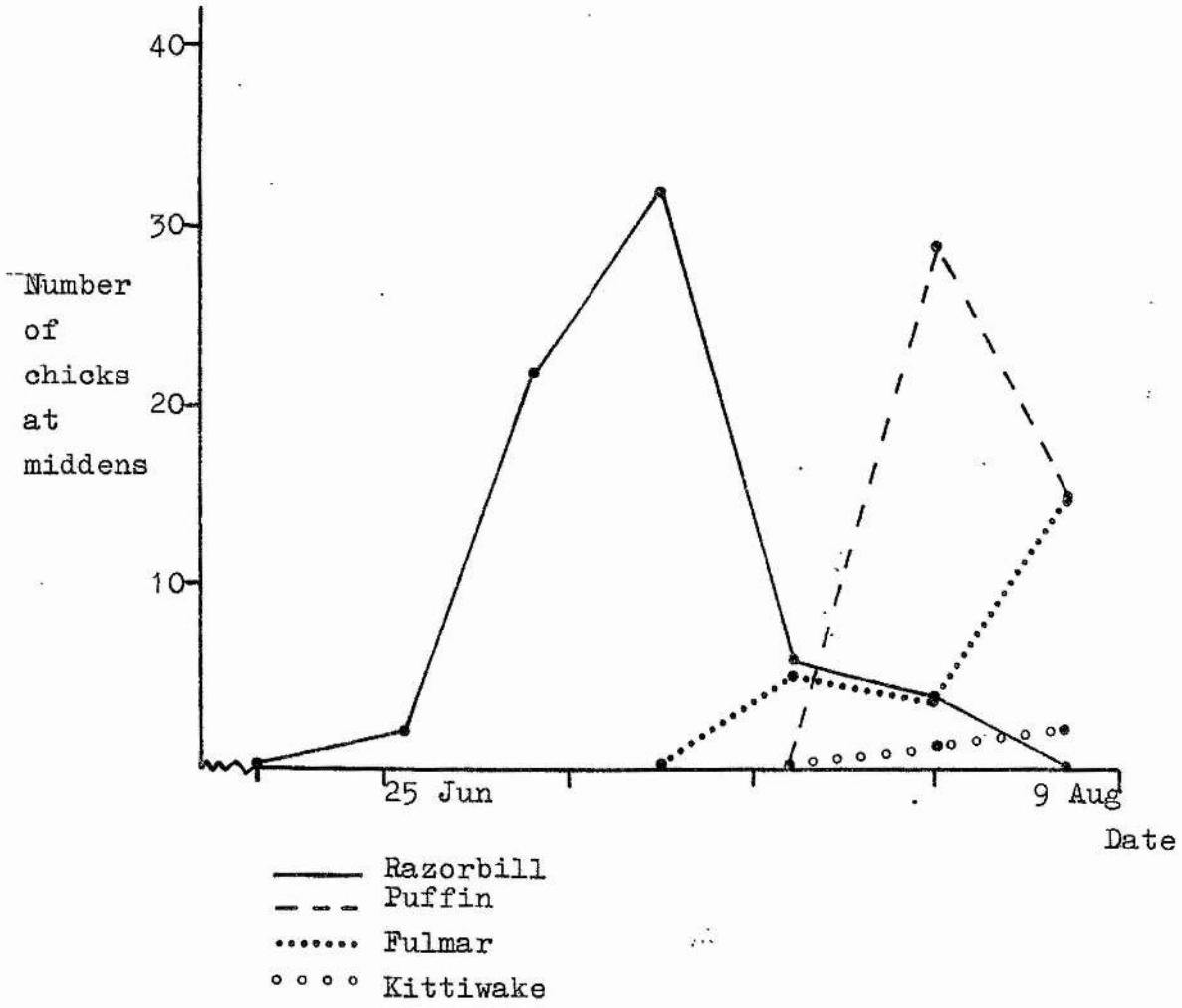


Fig. 1.15 Identifiable chicks found at middens in 1977

Table 1.14. Mortality of fledgeling Puffins attributable to gull predation in Sparse and Dense Areas, 1977.

SPARSE AREA	4,400 burrows	
	x 0.552	
	2,429 eggs	
	x 0.648	
	1,574 fledged	
12 killed	0.8% of total fledged	
DENSE AREA	13,000 burrows	
	x 0.827	
	10,751 eggs	
	x 0.838	
	9,009 fledged	
32 killed	0.4% of total fledged	

Significantly greater proportion of Sparse Area fledglings killed by gulls ($\chi^2 = 4.43$, $p < 0.025$)

In 1976 and 1977, gulls were only observed killing Puffin chicks during late July and early August. The chicks which were taken were large and had little or no down on their plumage, indicating that they were ready to fledge. Herring Gulls were seen taking smaller chicks from burrows earlier in the 1976, 1977 and 1978 breeding seasons. In 1978, L. marinus individuals were seen chasing Herring Gulls carrying downy Puffin chicks on a few occasions, but the outcome of these chases was not observed.

The temporal pattern of Razorbill fledgeling kills corresponded with the observed pattern of Razorbill fledging on Dun in 1977, peak kills between 12 July and 18 July coinciding with peak fledging on the island (Fig. 1.15). In 1978, Razorbill chicks were the only young birds found at middens in late June and early July. 31 Razorbill chicks were found between 25 June and 8 July 1978, compared with 24 found over the same period in 1977.

More than 15% of Razorbills estimated to be fledging from the Sparse area were killed by gulls in 1977, significantly more than the four percent of Dense area fledgelings killed in that year (Table 1.15).

Peak numbers of Razorbill fledgelings were found later in the Sparse area than in the Dense area. In 1977, over 40% of Dense area Razorbill fledgeling kills were found before 12 July, compared with less than 30% of Sparse area kills. In 1978, when data covered only the initial part of the Razorbill fledging period, 87% of all corpses were recovered in the Dense area. The majority of Razorbill fledgeling kills were found at eight middens. Middens 13 to 17 in the Dense area held 47% of kills in 1977 and 71% in 1978. One pair

Table 1.15. Mortality of fledgeling Razorbills attributable to gull predation in Sparse and Dense Areas, 1977

SPARSE AREA

300 sites

x 0.90

270 eggs

x 0.70

189 fledged

29 killed 15.3% of total fledged

DENSE AREA

1,400 sites

x 0.90

1,260 eggs

x 0.70

882 fledge

37 killed 4.2% of total fledged

Significantly greater proportion of Sparse Area fledglings killed by gulls ($\chi^2 = 31.56$, $p < 0.005$).

accounted for 27% of 1977 kills and 45% of 1978 kills. Three middens in the An Fhaing region of the Sparse area held 38% of the 1977 kill, but only 13% of the 1978 kill.

The remains of 24 Fulmar chicks were found between 19 July and 9 August 1977 at 11 middens. Eight of these middens were in the Sparse area and contained the remains of 16 chicks. No Fulmar chicks were found at middens in June and early July 1978. Kills in 1977 occurred prior to Fulmar fledging on Dun. Fulmar chicks were sometimes found sitting at middens away from Fulmar nesting areas, such as midden 33.

Discussion

The increasing contribution of young birds to the total biomass of avian prey caught by gulls reflected differences in the species of fledgelings caught, with Razorbills comprising the bulk of the first fledgelings caught, and heavier Puffin fledgelings and Fulmar chicks comprising most of the later kills.

The correspondence between the temporal distribution and abundance of young bird kills and the observed Puffin and Razorbill fledging periods indicates that gulls hunted the young of these species when they were most accessible. At the end of the nestling period, Puffin chicks often emerge from burrows to exercise their wings, making them more accessible to gulls, and eventually fly out to sea unattended by their parents (cf Lockley 1933). Razorbill chicks, which are mostly reared in crevices between boulders on Dun, are flightless when they leave their nests, and many have to scramble across large rocks before reaching the sea. During fledging, Razorbill chicks maintain auditory contact with one parent by calling loudly (Greenwood 1964). Thus the chicks' own behaviour and the

difficulties of negotiating obstacles en route to the sea may have made them both obvious and vulnerable to gull attack at fledging, but not earlier in the breeding season. Data from North Rona, Orkney and Skomer also indicate that gull predation on chicks of other seabirds is heaviest during the fledging periods of these other species (Corkhill 1973, Evans 1975, Beaman 1978). This is also the case in Glaucous Gull (Larus hyperboreus) predation of Little Auk (Plautus alle) and Brünnich's Guillemot (Uria lomvia) chicks and Great Skua (Catharacta skua) predation of Kittiwake (Rissa tridactyla) chicks (Lovenskiold 1954, Bateson 1961, B. Furness 1979).

The geographical distribution of Razorbill kills on Dun reflected the distribution of Razorbill breeding sites, most fledgelings being found at middens close to Razorbill sub-colonies. The different timing of peak Razorbill fledgeling kills in Sparse and Dense areas also indicates that gulls hunted these birds near their own nests. Razorbills fledge later from breeding sites with small numbers of breeding pairs than from sites with more breeding pairs (Lloyd 1976). Hence, fledgelings would be expected to have emerged later from the small Sparse area sub-colonies than from the larger Dense area sub-colony, and if Sparse area gulls killed Razorbill fledgelings near their own nests, peak Sparse area kills should have occurred after peak Dense area kills, as was the case in 1977.

Figures on the extent of gull predation on Dun Puffin chicks could have underestimated the real kill in a number of ways. Midden clearances stopped before the end of the Puffin fledging period, and hence did not record kills late

in the breeding season. However, since gulls began to disperse from Dun in early August, with very few carcasses of Puffin or other species found at middens at this time, this is unlikely to have severely underestimated the total kill of young Puffins. There are no data on how many Puffin chicks were killed by Herring Gulls. This predation merits further study, but since it was observed only occasionally, was again unlikely to have been responsible for a heavy mortality of Dun Puffin chicks. Productivity estimates for Dun Puffin burrows are based on data from study areas which contained only part of the total number of Puffin burrows on Dun. Figures on Puffin fledgeling production and mortality in Sparse and Dense areas thus indicate relative rather than absolute differences in the percentage of fledgelings killed in the two areas. These calculations almost certainly overestimate the percentage of Puffin fledgelings killed in the two areas, since gulls could have selected prey from areas outwith the burrow productivity study sites.

The number of Razorbills breeding at different parts of Dun is not known precisely, due to difficulties of censusing in boulder scree. There are also no data on the productivity of Dun Razorbills, so again, calculations of Razorbill fledgeling mortality indicate relative rather than absolute differences in the kill in Sparse and Dense areas. The figure of at least 15% of Razorbills fledging from the Sparse area in 1977 being killed by gulls is of the same order as the 17.5% of fledgeling auks observed killed by Glaucous Gulls on Bear Island in 1972 (Williams 1975). The percentage of fledgelings attacked, and the success of attacks declined with increasing numbers of young seen fledging per

thirty minute period on Bear Island. This suggests a 'confusion effect', whereby the hunting performance of Glaucous Gulls declined with increasing numbers of prey (see this study, Chapter Two, Final Discussion), and also indicates the benefits of synchronised fledging for young auks (Greenwood 1964). Such synchronisation could have influenced the observed differences in fledgeling mortality at high and low density Puffin and Razorbill sites on Dun.

Killing of large Fulmar chicks by gulls is unusual, the few records from other colonies being of very small chicks killed by various Larus species and swallowed whole (Fisher 1952). Such predation by Dun gulls could in part have been due to gulls having occasional access to chicks which were starving and had little or no oil for use in defence against predators, the chance of encountering such chicks perhaps being higher on Dun than at sites with a small Fulmar breeding population.

That local differences in the abundance of different seabirds may influence gull predation on young birds is suggested by observations I made on Grimsey in July 1979. Kittiwakes formed the bulk of gull prey in Grimsey middens (Section 1.4, Table 1.6). Gulls at one Grimsey study site had access to many young Kittiwakes which fell from high density nesting sites down to a boulder beach. On several nights gulls were observed feeding on Kittiwake carcasses, and did not attempt to take Razorbill chicks which were fledging from the boulder beach, even when such chicks passed within a few metres of a gull and took more than half an hour to join their parents in the sea.

Data presented here indicate that contrary to previous suggestions, gull predation is not responsible for a heavy mortality of Puffin fledgelings on Dun. Predation on Razor-

bill fledgelings appeared to be more serious, but requires more detailed data on Dun Razorbill numbers and productivity for proper assessment. In general, data from Dun and elsewhere indicate that the young of other seabirds are at highest risk of predation from gulls when fledging, and that the extent of this predation is influenced by local differences in breeding density, and by differences between colonies in the relative numbers of different seabird species breeding there.

CHAPTER TWO

The hunting behaviour of L. marinus on the island of Dun

Plate 2.1 Gull on vantage point during a period of high Puffin wheeling activity

"The Greater black-backed gull is a big, handsome, ugly - faced creature and a very important bird in every way."

F. Fraser-Darling and J. Morton Boyd

'The Highlands and Islands'

Fontana New Naturalist, 1969

INTRODUCTION

There is no quantitative information available on the behaviour of predatory L. marinus. L. marinus breeding on Dun fed almost exclusively on Puffins. Pairs which caught fewest Puffins early in the breeding season failed to raise chicks. These failures, together with evidence on nest spacing and differences in the age of Puffins found dead at middens, suggested that different gull pairs used different feeding areas. Such behaviour might restrict the number of gull pairs feeding and breeding on the island and by extension limit the number of Puffins killed by gulls in any one breeding season. Field observations of L. marinus hunting behaviour are thus a crucial extension of the ecological study.

METHODS

Most detailed observations were of gulls hunting over the eastern part of Dun in June and early July 1978, around and east of an observation point about 120m a.s.l. on Puffin Transect Nine (Harris and Murray 1977). Observations were also made of gulls hunting over the western part of Dun from a site at Ruival on Hirta in 1977. Figure 2.1 shows observation points and the extent of the two study areas.

Gull hunting behaviour was recorded by focal animal sampling (Altmann 1974). A gull was chosen as a focal subject if it was seen attacking a Puffin in flight. The gull was then observed continuously until it caught and killed a Puffin, or landed without making a kill and made no further attacks within within five minutes. A 'hunt' was defined as a period of

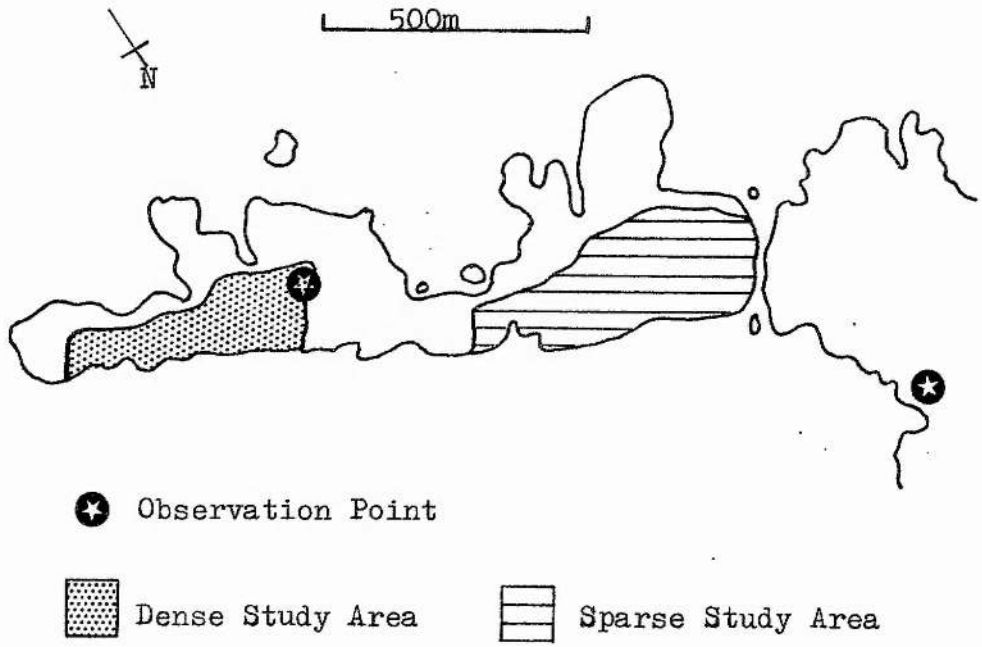


Fig. 2.1. Gull hunting behaviour study areas on Dun

gull activity during which the gull made at least one flight attack on a Puffin before landing and made no further attack flights within five minutes of landing.

Observations were dictated onto cassette tape and later transcribed to give accurate timings of hunts and hunt behaviour.

In each observation period, middens and nests used by each focal gull were noted. Where gulls hunted and where they interacted with other gulls was recorded by reference to topographic features and to the number coding of Puffin colony transects (Harris and Murray 1977). Movements were later plotted on a 1:1600 scale map overlaid with grid squares of size 16 by 16 metres. Use of grid squares was scored on a one-zero basis for each sequential five second period of a recorded hunt to indicate both overall ranging and frequency of use of squares by a hunting gull.

Attacks on Puffins were classified as 'encounters'. Class 1 encounters were where a gull made a movement towards a Puffin but did not press home the attack. Class 2 encounters were where the gull narrowly missed its target. Class 3 encounters were where the gull caught a Puffin but the prey escaped. Class 4 encounters resulted in a kill.

In each observation period the number of gulls seen hunting was recorded both by scans of the study area at the end of each hunt by a focal gull and by noting the presence of other hunting gulls during a hunt by a focal gull.

The number of Puffins flying in a study area was classified as 'low', 'moderate', 'high' or 'very high', variations in numbers being noted as they occurred. These classifications were standardised by cassette recorded sample counts

of birds flying across a 10 x 50 binocular field of view made from the same location for different density classifications.

During three nights spent on Dun gulls were never seen to hunt. From this, and similar information from other observers (M.P. Harris pers. comm.) it was assumed that gulls did not hunt at night, and watches were made during daylight hours accordingly. Observations were made during all hours of daylight in watches of two to ten hour duration.

The term 'wheel' as used in this chapter refers solely to the usual type of Puffin flock seen flying over Dun. Individuals in a wheel flew in a broad elliptical track over part of the colony and the adjacent sea area, flying into the wind over land and with the wind over the sea. This behaviour is quantified in Chapter Three.

RESULTS

2.1 THE FORM OF GULL HUNTING BEHAVIOUR

All Puffin kills took place after the Puffin had been caught in the air. Occasionally a Puffin being pursued by a gull would plummet to land and dive down a burrow. The gull then followed and searched the area for a short time. Such hunts were always unsuccessful.

Gulls often stood on vantage points such as rocky spurs, near their nests. Hunts often commenced with the gull flying up from such a lookout point and circling an area where Puffins were flying in front of the colony. The gull slowly spiralled up to several hundred metres, circled

and then stooped, with wings held stiff and partially folded, towards a flying Puffin. Pursuits of several Puffins might follow in quick succession. A Puffin which plummeted from a wheel and flew out to sea was sometimes pursued by a gull for a few hundred metres until it either outflew the gull, or landed in the sea and dived. The gull then gave up the hunt.

Members of a pair sometimes hunted together. One bird circled above the colony and the other panicked Puffins standing at the colony into flight by flying low over the colony and calling. This seemed to be a specific behaviour. Gulls hunting singly would also on occasion fly low over the burrow slopes, calling.

A Puffin was caught by being gripped in a gull's beak. Once caught, the Puffin was often able to bite the gull while being carried in flight. It appeared that the Puffin was less able to bite the gull, and less likely to escape in the air, if caught by the neck. After a catch, the gull would usually take the Puffin to a regular killing place, often near the nest. Here the Puffin had another chance to escape when the gull attempted to kill it.

Puffins were killed by being stabbed through the chest, this normally happening two or three minutes after the gull landed with its catch. The gull would then feed for 20 to 30 minutes before letting its mate feed. Chicks were fed by regurgitation near or at the nest, and the carcasses of Puffin prey were not usually removed from middens.

Once, a fresh corpse was stolen by a gull from a neighbouring pair while the killer was changing over with its mate.

After an aerial dispute, the killer and its mate regained the corpse. The corpse thief in this case was a bird from pair 13. This was the only nest where it was known that at least one member of the pair habitually removed corpses from the middens of other pairs, although pair 13 also killed Puffins for themselves.

An agonistic encounter was where one gull rapidly flew after another and glided alongside. The two gulls then flew together for a short distance before one banked away and flew back to the area where agonism had initially occurred, or down to a nest. These 'agonistic glides' were not accompanied by overt aggression, such as the birds pecking at each other in flight.

Discussion

Catching behaviour differed from that described for other areas, or for St Kilda in the past, where gulls have been observed searching burrow entrances on the ground to grab emerging Puffins (e.g. Lowe 1913, Williamson 1958, Williamson and Boyd 1960). The high vegetation in many parts of the Dun Puffin areas might restrict gull visibility and movement on the ground, thus reducing the effectiveness of hunting. However, since gulls on the neighbouring island of Boreray, where vegetation in Puffin areas is close cropped by sheep, were observed behaving during some hunts in a manner which panicked Puffins into flight, vegetation cover cannot be the only reason for these differences in hunting behaviour.

Dun is one of the few gull breeding areas in Britain documented to date where all gulls subsist almost entirely

on Puffin prey. While a ground searching hunt style might be used occasionally by gulls which did not rely on Puffins as major prey, this method of hunting could be precarious for gulls which depend on catching Puffins regularly throughout the breeding season. Unless a gull could determine burrow occupancy from cues not apparent to human observers, waiting at burrow entrances for emerging Puffins could be a time consuming method of hunting. When Puffins are flying, gulls have knowledge of prey location and can decide on this basis when to make attacks.

The form of agonism between flying gulls during hunt periods may indicate that serious disputes over hunting space are settled very early in the breeding season. In the absence of any detailed accounts of L. marinus ethology this interpretation of observed agonism would require further field observations early in the breeding season for its assessment.

2.2 PUFFIN AIR DENSITY

All classifications of numbers of Puffins flying in the Dense study area were significantly different from each other in actual Puffin numbers (Mann-Whitney U $P \leq 0.0001$) (Fig. 2.2). The difference between 'low' and 'very high' Puffin number classifications represented at least a fourteen-fold increase in real numbers in the Dense study area. Numbers of Puffins flying in the Sparse study area were classified relative to that area. Each Sparse area number classification was equivalent to the next lowest classification of numbers in the Dense area. For example, 'very high'

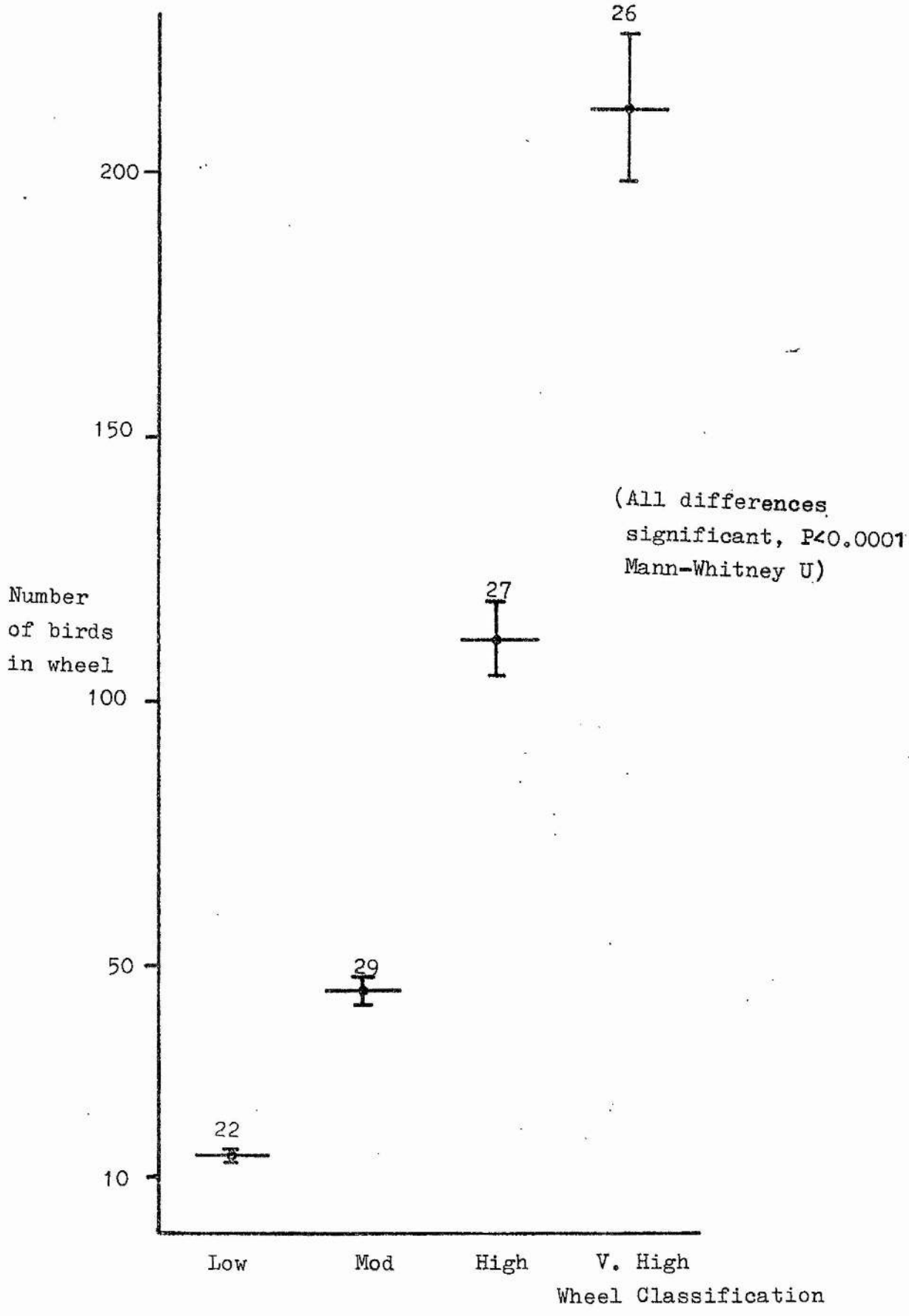


Fig. 2.2 Number of Puffins in different classes of wheel

Sparse area classifications were equivalent to 'high' Dense area classifications.

2.3 GULL HUNTING RANGES

In these descriptions 'hunting range' is the area containing the hunting places of a pair of gulls. 'Core area' is the area of heaviest regular hunting use within the hunting range. A core area was defined as the area within which each complete 16 by 16 metre grid square included more than two percent of the total square use records by a hunting gull or gulls from a known nest in a number of hunts over several days. (Mean hunts per home range = 7.29 ± 1.22, Mean hunt days per home range = 3.86 ± 0.08, $N = 7$ nests.) This arbitrary definition of core area complies with the methodological recommendations of Jennrich and Turner (1969).

The core area used by gulls from any one nest was similar in different hunts throughout the 1978 study period, as illustrated for three hunts from Nest 15 in June and July (Fig. 2.3).

All the colony was hunted over by gulls, and there was considerable overlap of hunting ranges. For example, the study area was regularly covered by three adjacent pairs from Nests 13, 14 and 15 (Fig. 2.4). Despite this overlap, individual pairs hunted mainly in different areas. This is shown in a map of core areas (Fig. 2.5). However, no core area was used exclusively by one pair. On average, more than a third of any one pair's core area was shared with two to three adjacent core areas.

Spatial overlap of core areas was not necessarily asso-

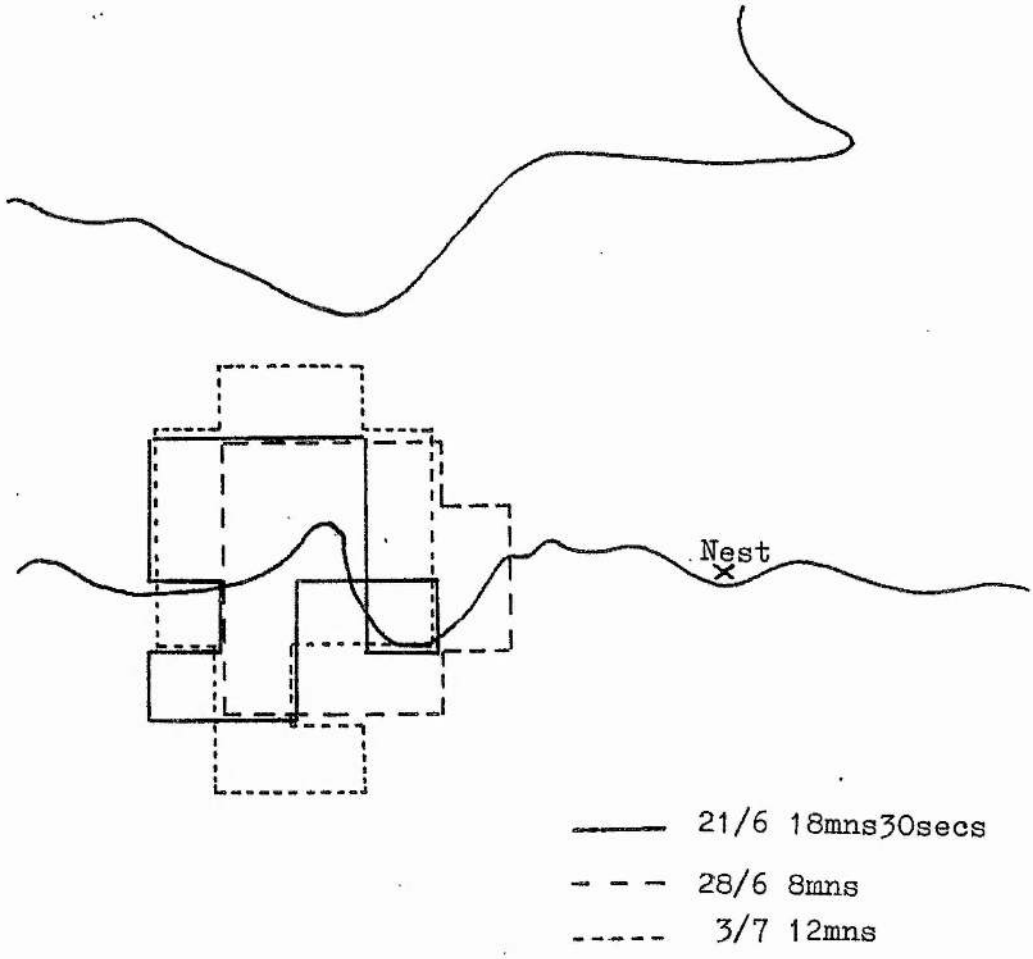
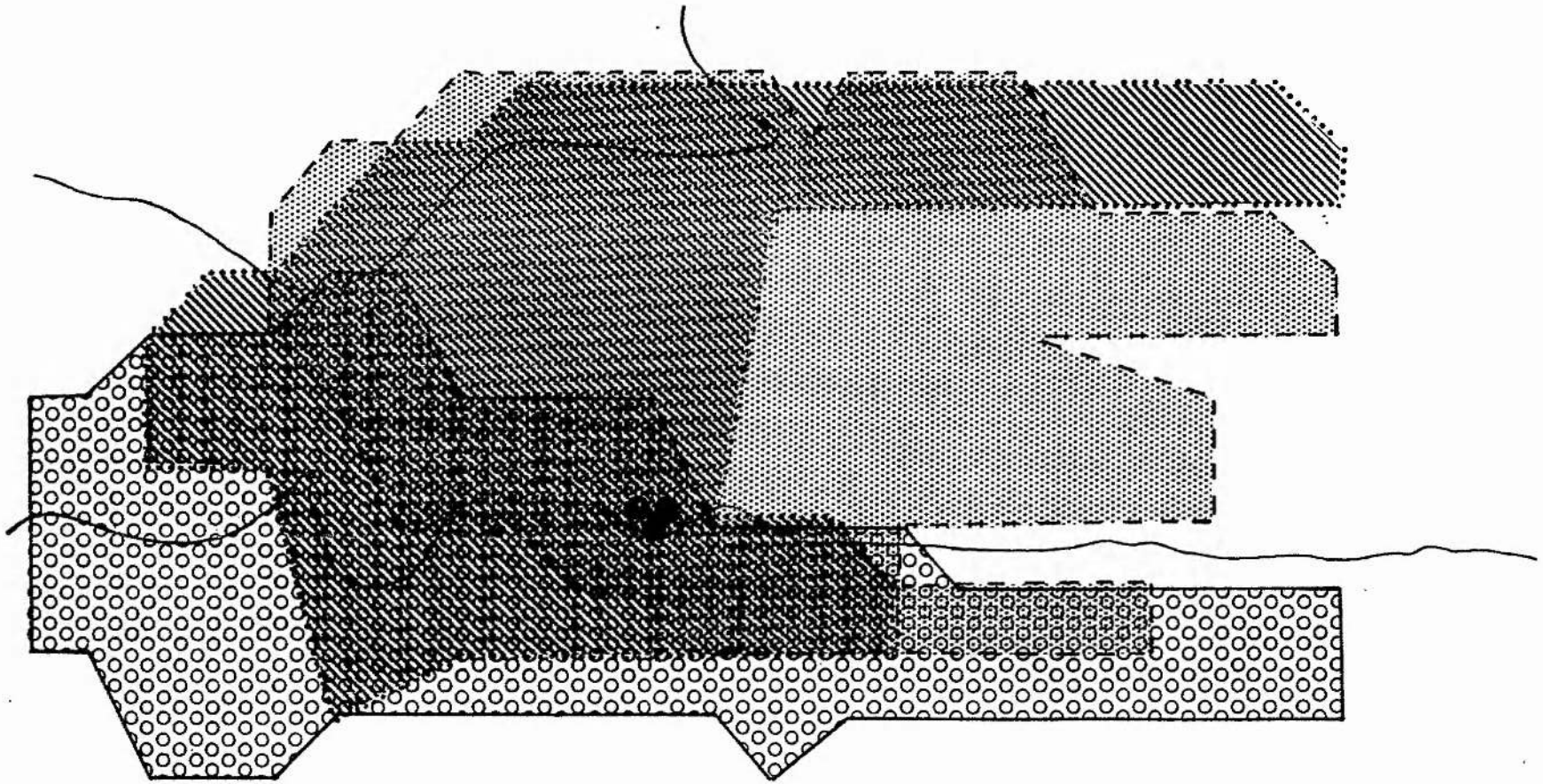


Fig. 2.3 Core hunt ranges in three hunts by gull from Nest 15, June and July 1978



——— 15

..... 14

– – – 13

✪ Nest

Fig. 2.4 Hunting ranges of gulls from Nests 13-15, 1978

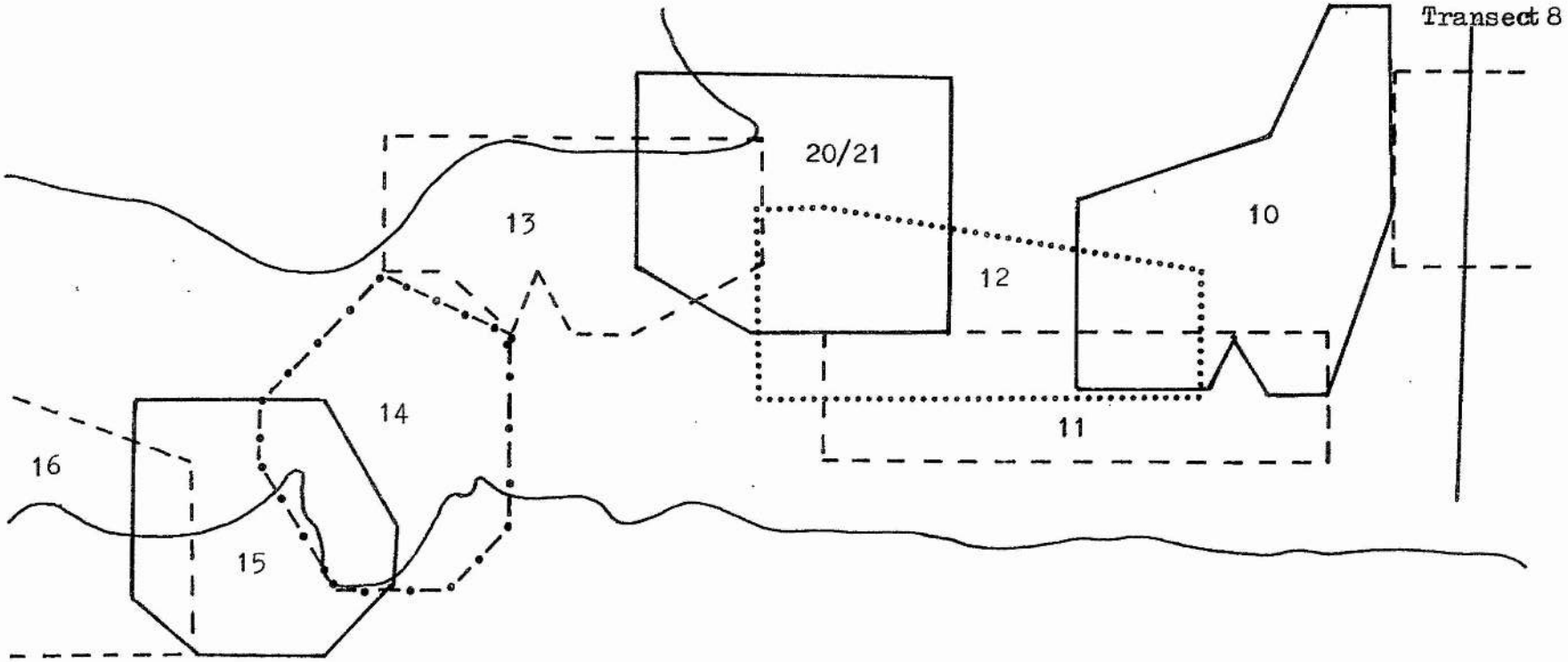
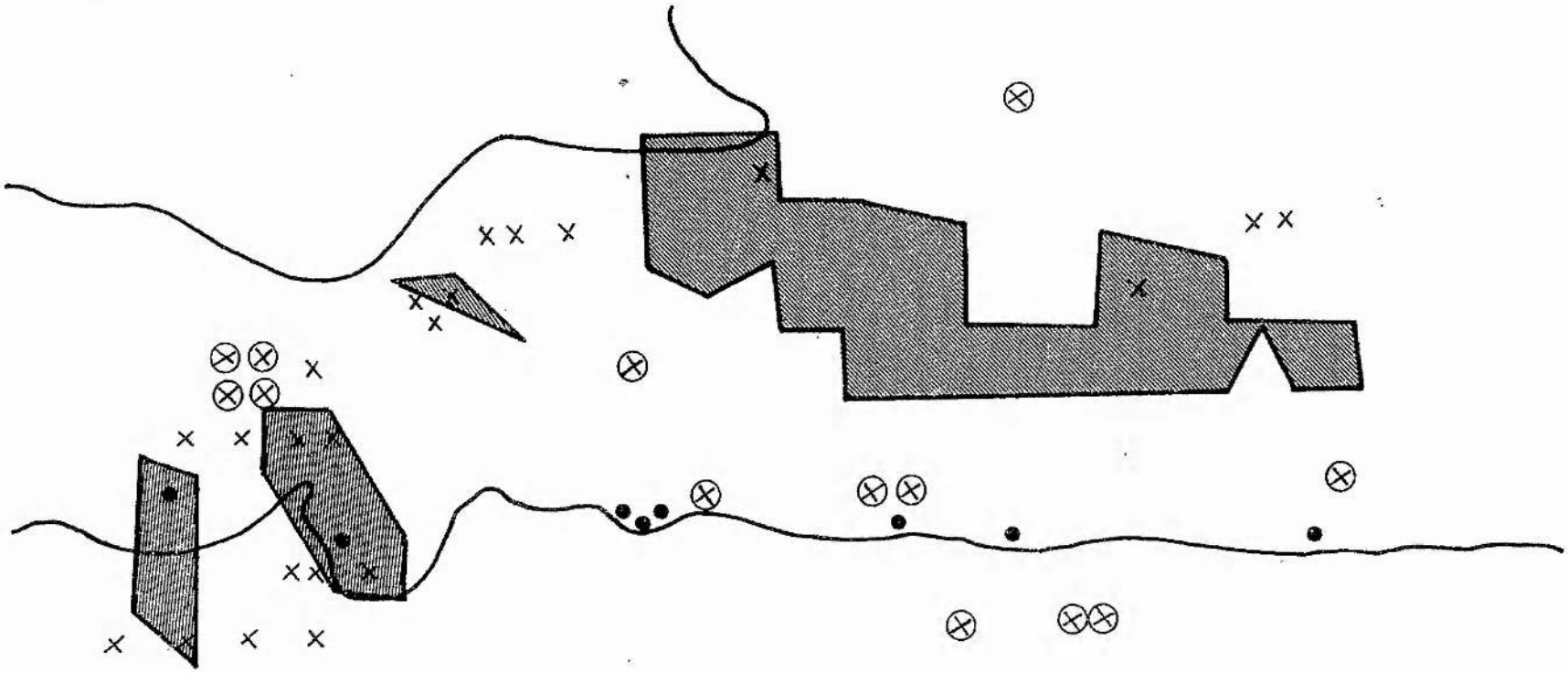


Fig. 2.5 Core hunt areas of gulls in Dense Study Area, 1978 (Scale 1:1600)

ciated with temporal overlap of use by different pairs. For example, overlapping core areas 11 and 12 were never hunted simultaneously. In a number of instances, a gull began hunting within five minutes of a gull from a neighbouring pair ceasing hunting, the former gull having remained on the ground for the duration of the latter's hunt. Regions of core area overlap, and the position of agonistic hunting disputes within and outside core areas are shown in Fig. 2.6. There was no significant association between areas of core area overlap and agonism sites ($\chi^2 = 1.66$ $P>0.10$), nor was agonism more likely in core areas than other areas ($\chi^2 = 0.525, P>0.10$). The percentage of its core area a pair shared with other gulls was not correlated with the frequency of agonism while hunting ($r_s = 0.643, N = 7\ P>0.05$).

For 32 cases of agonism between two gulls where the initiator of the dispute was known, 68% were initiated by the hunting bird being monitored and 32% were initiated by the other gull. In 70% of cases where the hunter was attacked the hunter landed or flew out of the study area within one minute. By contrast, in 95% of cases where the hunter initiated agonism the hunter remained in the air and kept hunting for more than one minute. Agonism between flying gulls during hunt periods thus usually resulted in one gull leaving the area where agonism occurred. Most instances of agonism outwith core areas at coastal sites illustrated in Fig. 2.6 occurred near nests and so were probably related to nest defence.

Gulls tended to concentrate hunting effort away from their own nest. The nest, hunting range and core area used by pair 15 illustrates this dissociation of nest site and main



Core Overlap

Core Agonism

Non-Core Agonism

Nest

Fig. 2.6 Gull agonism and core area overlap

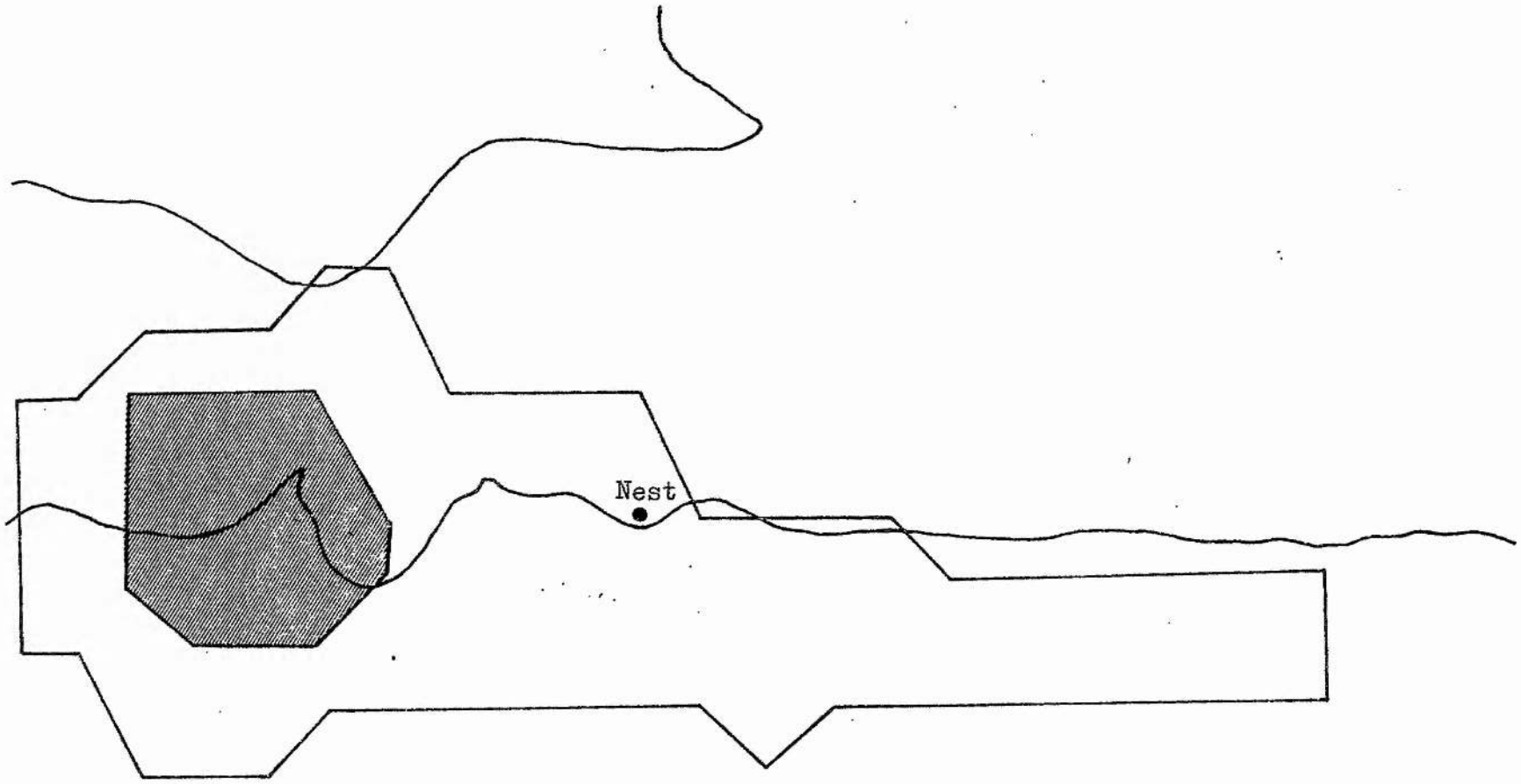


Fig. 2.7 Hunting range and core area of gulls from Nest 15, 1978 (Core Area shaded)

hunting area (Fig. 2.7). Coastal movements away from the core area for this pair were usually pursuits of Puffins which started in the core area, but ended over the sea, and were not systematic patrols of coastal areas.

The mean size of core areas for seven pairs whose core movements fell entirely within the study area was 4086 m^2 ± 198 m^2). Dun has an area of 32 hectares (Harris and Murray 1978), so there could be 78 exclusive core hunt areas on Dun. If at least one third of each core area was shared with other core areas, there could be at least 104 core hunt areas on the island.

Discussion

The dearth of core hunting areas over most of the near coast regions in the study area might be due to nest defence, as most gulls nested near the coastline. Concentration of hunting away from own nests, but near the coastline, might thus not have been feasible due to harassment from gulls at other nests. Gulls may also have been inhibited from hunting near their own nest. This appears to be the case in some raptors. Many species of bird nest close to breeding raptors, and one species, the Red-breasted Goose (Branta ruficallis) often nests near breeding peregrines (Falco peregrinus), a species which sometimes feeds on geese (Durango 1949, Kretschmer 1965).

On the basis of the observed overlap of core areas, 78 exclusive core areas for the whole island might be an underestimate of possible core areas. This could be reduced if there was indeed a tendency to avoid coastal hunting over some stretches or if other areas of the island were not

equally suitable for hunting.

Data illustrating whether any aspects of Puffin density or behaviour influence gull hunting are thus essential for estimation of the possible number of gull hunting areas on Dun.

2.4 SPATIAL AND TEMPORAL FEATURES OF GULL HUNTS

Encounters with Puffins in the overall hunting area used by a pair of gulls were concentrated in the core area. (Hunting ranges 11, 14, 15: = 224 encounters; mean percentage of encounters in core areas = 69% ± 1%). This is partly because the core area is by definition where gulls spent most time while hunting. However, within core areas there was local clustering of encounter locations. (Figs. 2.8, 2.9, 2.10).

The only factor which obviously influenced encounter locations in some hunting ranges was where Puffins turned in to fly over land, or out to fly over the sea in a wheel. For example, 70% of all encounters, and 81% of core area encounters in Hunting range 11 occurred at the two turn regions of a single wheel. This concentration of encounters at wheel turn regions in Hunting range 11 is highly significant (core area : $\chi^2 = 30.25$, $P < 0.01$) and was obvious in the field. Similarly, 61% of all encounters and 72% of core area encounters in Hunting range 15 occurred at a single wheel turn region (core area : $\chi^2 = 7.77$, $P < 0.01$). (The amount of core area space falling in and out-with turn regions was used to generate expected + turn, - turn encounter numbers in these calculations.) Encounters in home range 14 were rather more

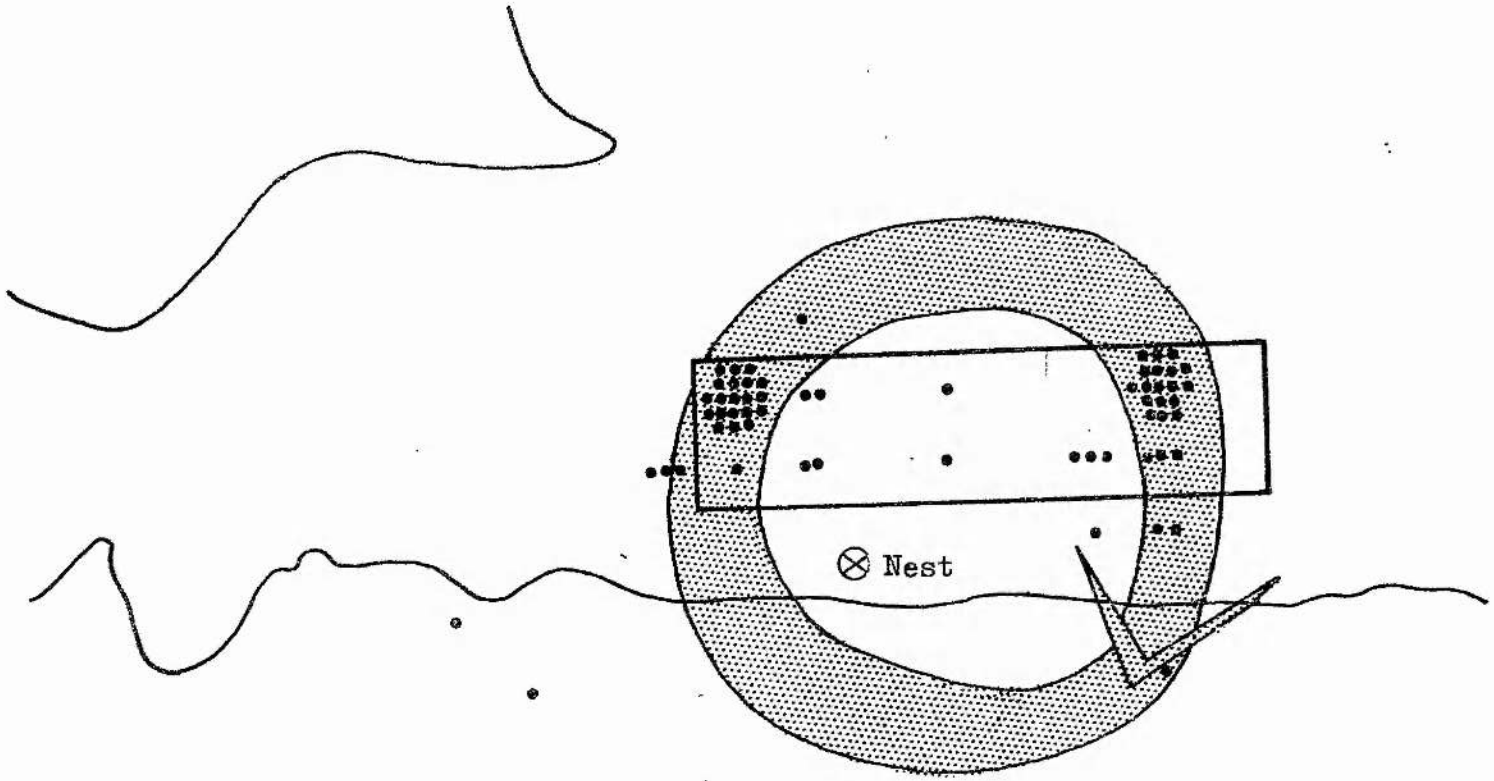


Fig. 2.8 Location of 65 encounters in Hunting Range 11

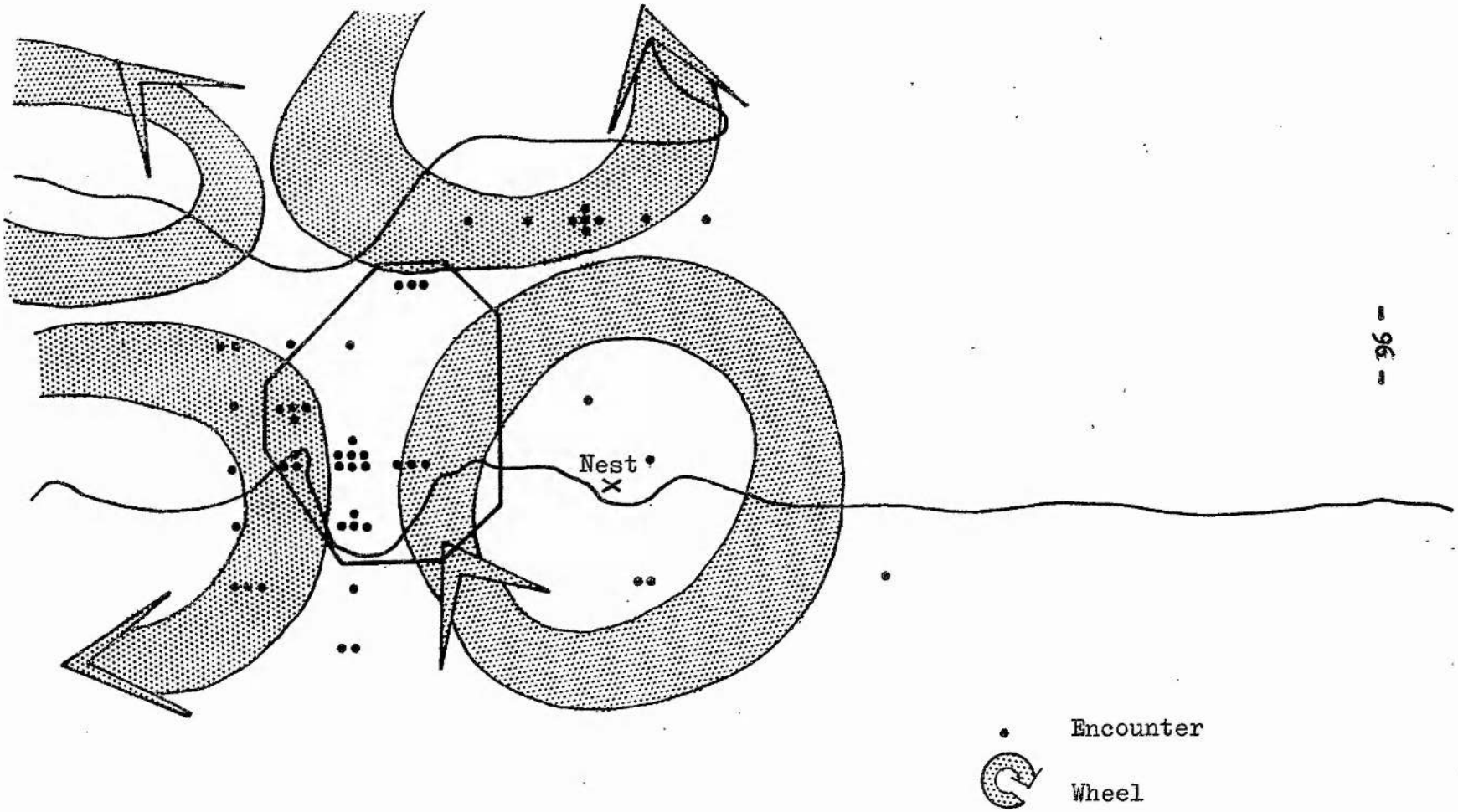
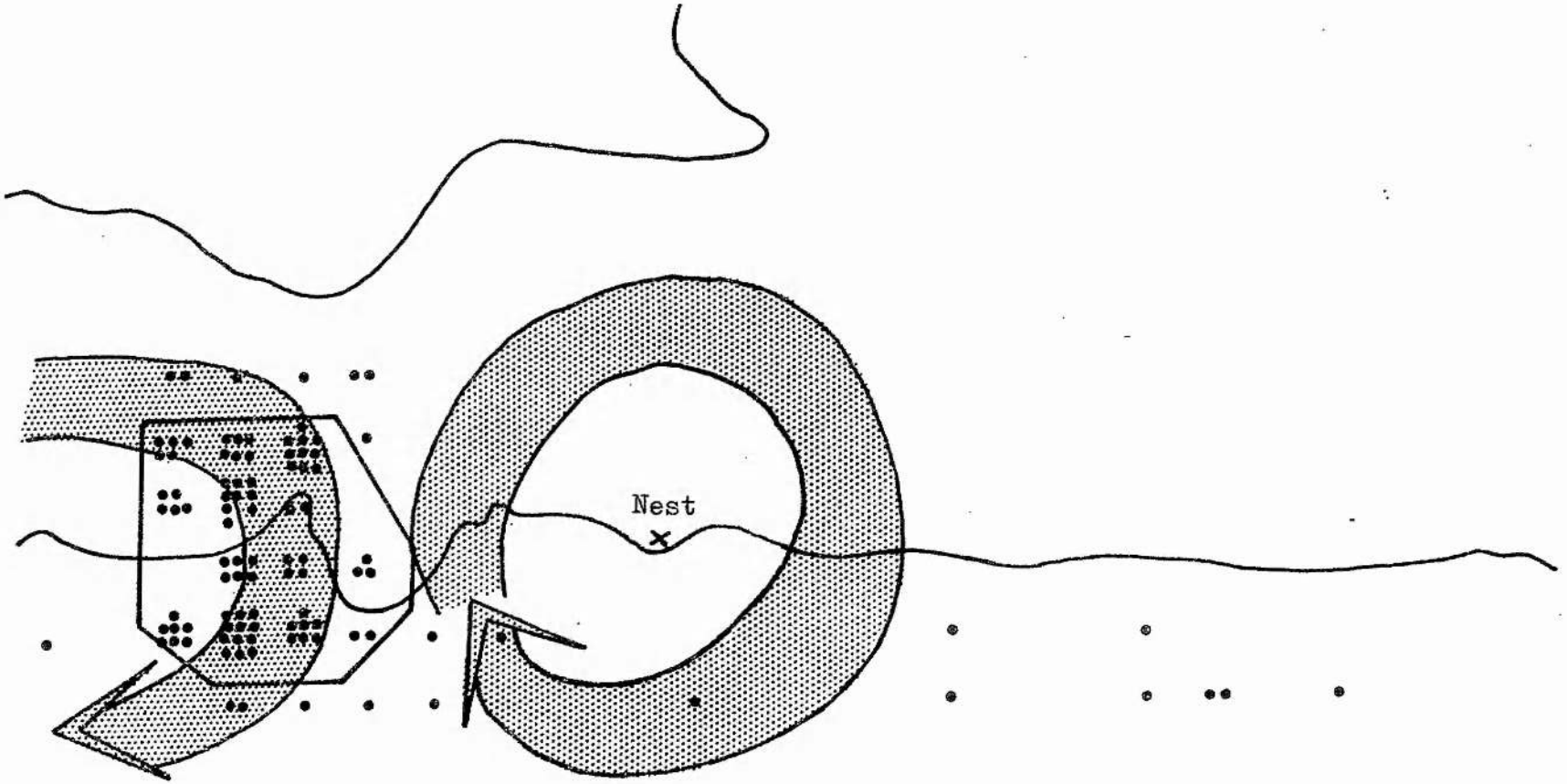


Fig. 2.9 Location of 53 encounters in Hunting Range 14



Wheel

Encounter

Fig. 2.10 Location of 106 encounters in Hunting Range 15

scattered. Only 51% of all encounters in this hunting range occurred within the core area, there being no significant association between core area encounter location and wheel turn regions ($\chi^2 = 1.19, P>0.1$).

The distribution of core areas was associated with the distribution of wheel turn regions. Of ten wheel turn regions in seven different wheels within the study area, eight were included in known core hunt areas. The other two turns were adjacent, at an area to the extreme S.E. edge of the study area which may have been hunted by gulls using nests in the Fort area whose core areas were not known.

All core hunt areas included at least one wheel turn region (mean = 1.86 ± 0.34 turn regions). Two wheels falling entirely within the study area were each partly included in the core hunt areas of three different gull pairs.

Wheel turn regions covered 31% of the study area, and wheel tracks as a whole 63%. These figures were used in further analysis of gull agonism locations to generate expected numbers of agonistic disputes falling within wheels and turn regions. Agonism was significantly associated with wheel turn regions ($\chi^2 = 3.71, P < 0.05$, 1-t, $N = 35$) and with wheels as a whole ($\chi^2 = 4.97, P < 0.025$, 1-t, $N = 35$). 57% of agonism occurred at wheel turn regions, and only 11% occurred outwith wheel areas. A hunting gull threatened by another gull usually landed. Thus, the association of agonism with wheels implies that there was more competition between gulls for hunting space in wheel regions than in other areas, and that some characteristics of wheeling Puffins, especially at wheel turn regions, may have allowed efficient hunting.

Concentration of hunting at wheels and wheel turns suggests

that gull encounters with Puffins might be spatially predictable. The temporal patterning of encounters was analysed to assess whether gulls whose behaviour was predictable in space might distribute encounters, or successive visits to the same air space randomly in time.

The mean time interval between successive encounters during hunts was between 30 and 53 seconds for five different hunting ranges. (Fig. 2.11) The precise temporal distribution of hunting encounters for four hunts in home range 15 showed no significant deviation from random, as judged by the fit of the data to an expected Poisson distribution, for 30, 60, 120 or 180 second time windows (Fig. 2.12). This was also the case for encounters during five hunts in hunting range 11. The temporal patterning of encounters in hunting range 15 illustrates the tendency described earlier for gulls to sometimes make several attempts to catch Puffins in quick succession. Thus, for these hunting ranges encounters were spatially clustered but temporally random. Encounters in hunting range 14 appeared to be more regular in time (Fig. 2.13). The distribution of encounters in this hunting range was significantly different from random using a 60 second time window ($\chi^2 = 27.92, p < 0.001, 1 df$). Thus, for this hunting range, encounters were scattered in space, but appeared non-random in time. The observed and expected numbers of encounters in 60 second windows for hunts in ranges 11, 14 and 15 illustrate this analysis (Fig. 2.14).

A similar type of time analysis was used to assess whether visits to areas where many encounters took place were randomly distributed in time for the two hunt ranges with spatially clustered encounters. Birds hunting the two ranges

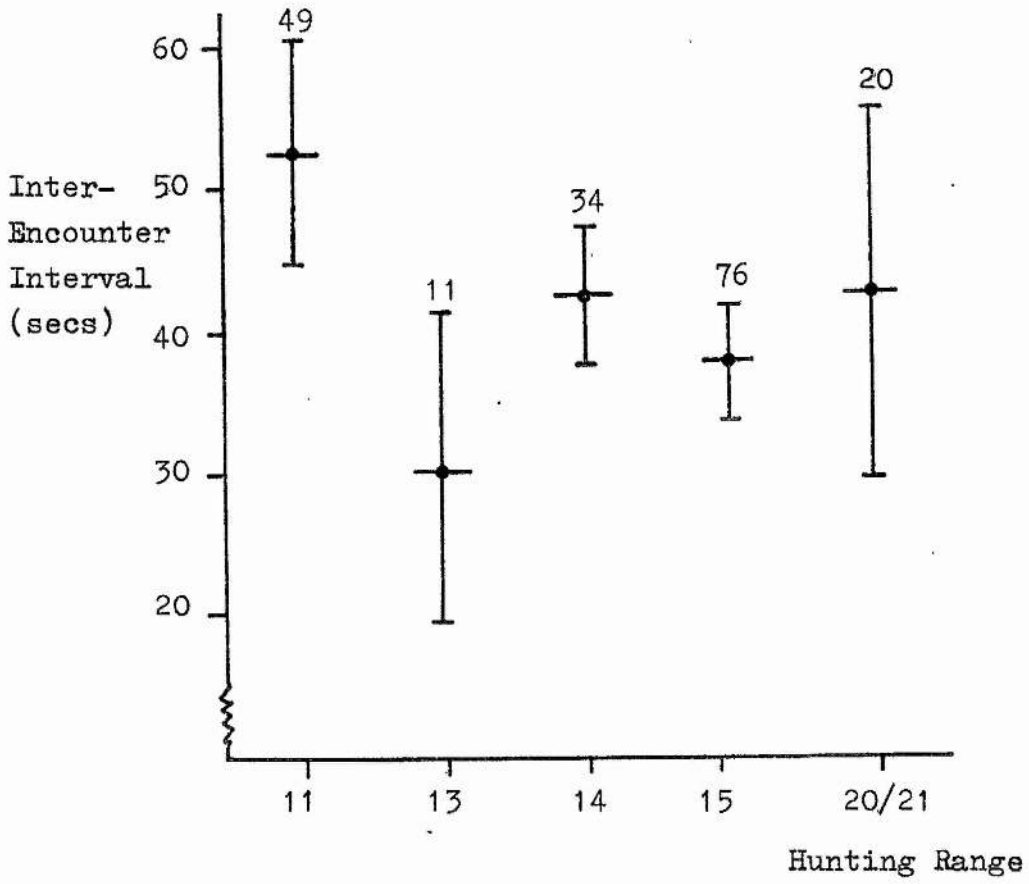


Fig. 2.11 Inter-encounter intervals in five hunting ranges (24 hunts, 135 hunt minutes)

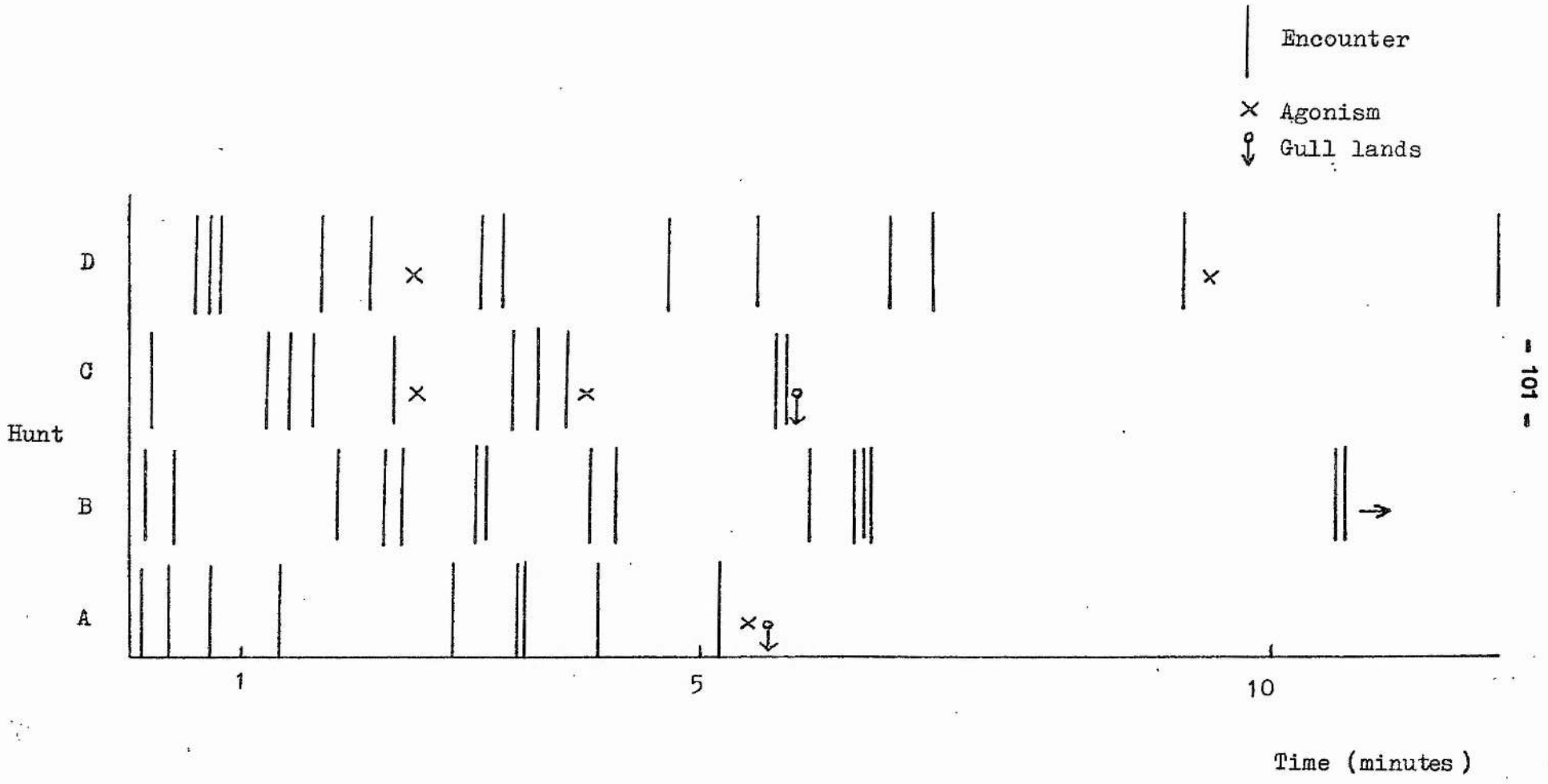


Fig. 2.12 Temporal pattern of encounters in four hunts in Hunting Range 15
(no significant deviation from random timing for 30,60,120,180 second windows)

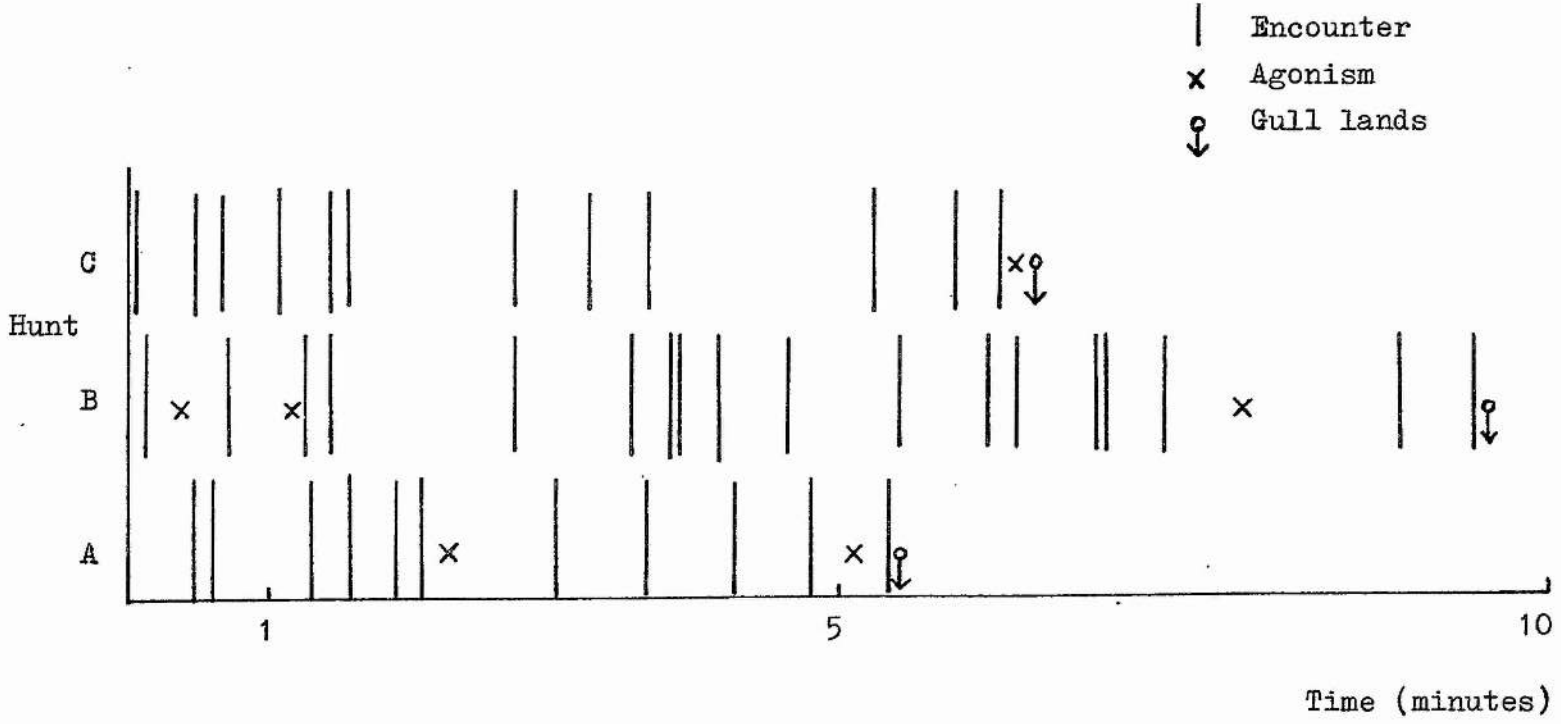


Fig. 2.13 Temporal pattern of encounters in three hunts in Hunting Range 14 (significant deviation from random timing for 60 second window, P 0.001)

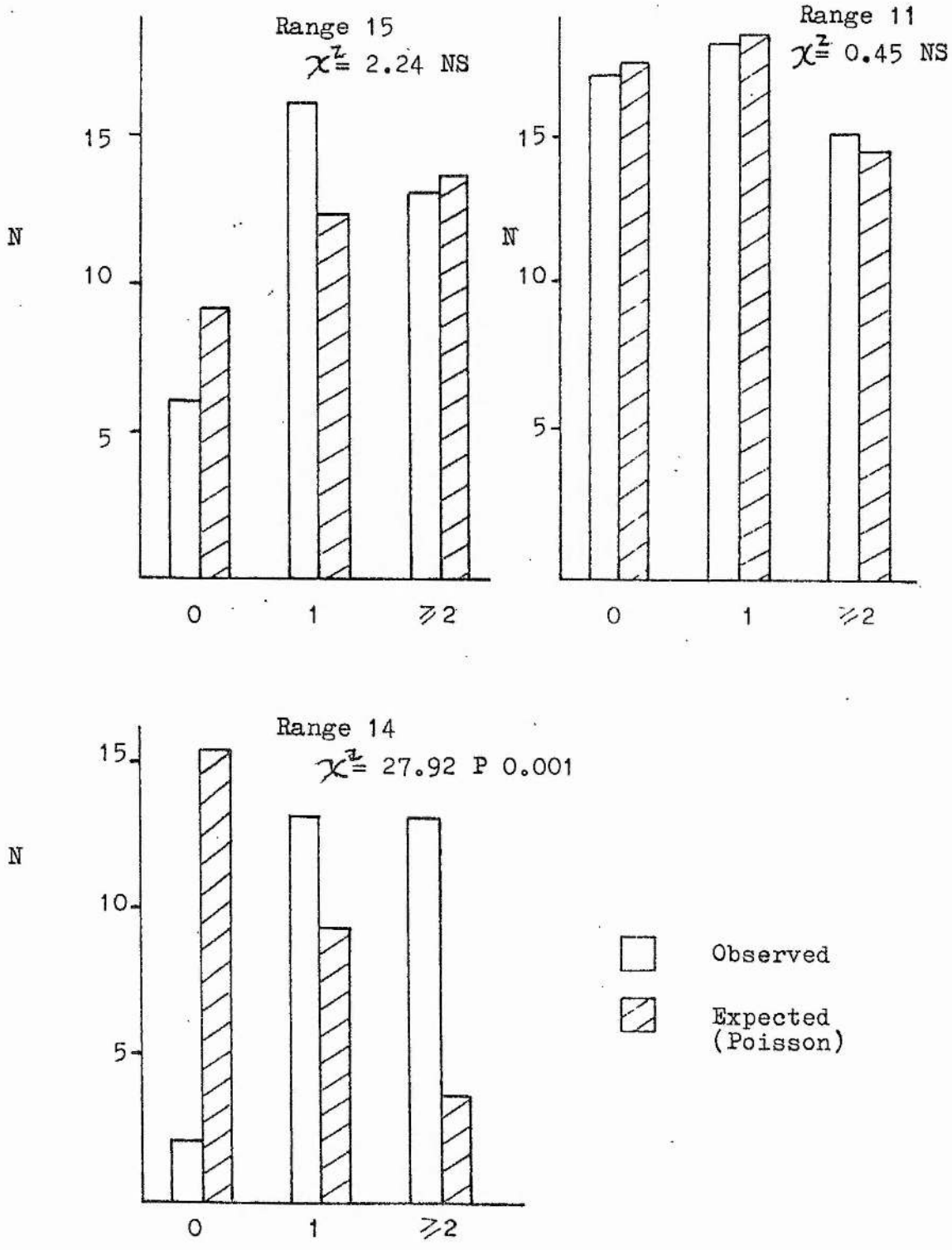


Fig. 2.14 Observed and expected distributions of encounters during 17 hunts in three hunting ranges (1 minute time window)

differed in the frequency of their visits to areas where many encounters occurred. The mean interval between visits to each of two areas in hunting range 15 was more than two minutes (Area 15a $\bar{x}$ = 134.7 $\pm$ 20.3 seconds, 27 visits, 5 hunts; Area 15b $\bar{x}$ = 157.6 $\pm$ 18.8 seconds; 24 visits, 5 hunts: t = 0.823 N S P>0.1). In contrast the interval between visits to each of two areas in hunting range 11 was on average less than one minute (Area 11a $\bar{x}$ = 36.9 $\pm$ 3.6 seconds, 80 visits, 5 hunts; Area 11b $\bar{x}$ = 41.6 $\pm$ 4.0 seconds, 63 visits, 5 hunts; t = 0.879 N S P>0.1). The timing of visits to the two hunting range 11 areas was significantly different from random using a 30 second time window, but not different using other windows (Table 2.1). Visit timing to one of the hunting range 15 areas was significantly different from random using a 120 second time window and the highest, but not significant, χ^2 value for the other hunting range 15 area was also found with a 120 second window. Deviations from random in both hunting ranges were mainly due to there being too many time cells observed as having one visit than would be expected if the timing of visits followed a Poisson distribution. Since these deviations were associated with time windows close to the mean observed inter-visit duration, there was an element of regularity in the gulls' ranging behaviour in core hunt areas.

Discussion

Although a hunting gull's movements might be to some extent predictable, attacks on Puffins, when defined in terms of time and space jointly, were unpredictable.

A concentration of L. marinus attacks on Puffins at wheel turn regions has previously been noted in Russia (Skokova 1962).

Table 2.1 Deviations from random (Poisson) in visit timing to same home range areas by hunting gulls

Home range	Area	$\bar{x}$ Inter-Visit	SE	Time window	χ^2	P
11	11a	36.9	3.6	30	6.66	<0.01
				60	0.66	NS
				120	0.48	NS
	11b	41.6	4.0	30	5.63	<0.05
				60	3.69	NS
				120	1.70	NS
15	15a	134.7	20.3	30	0.41	NS
				60	0.73	NS
				120	2.62	NS
	15b	157.6	18.8	30	0.29	NS
				60	0.37	NS
				120	4.05	<0.05

The fine structure of Puffin wheels is described in the next chapter, but a possible explanation for the association between encounters and wheel turn regions is given here. Puffins in wheels tend to fly with the wind over the sea and into the wind over land. Turning against the wind at wheel turn regions may reduce a Puffin's flight speed. Also, since turn regions of a single wheel are often close to turn regions of neighbouring wheels there is frequently a two-way traffic of flying Puffins at these areas. Although more work is needed on this subject, flying a chosen course may thus be more difficult for a Puffin at wheel turn regions than at other parts of a wheel. This difficulty might make the Puffin more vulnerable to gull attack at these regions.

For gulls, the opportunity to exploit vulnerable Puffins at wheel turn regions might be more than simply a bonus accruing from chance association of hunting range and wheel. The association between agonism and wheel turn regions suggests greater competition for air space containing a wheel than for other areas. This could imply that for many gulls, the real hunting 'territory' is a wheel or wheels rather than the region arbitrarily classed as a core hunt area in this study. If so, the number of Puffin eating gull pairs which Dun could support might be a function of the number of Puffin wheels there.

21 different wheels were recorded on Dun in both 1977 and 1978 (see Chapter Three). Within the study area, each wheel was hunted by three different gull pairs. Assuming the same for other wheels, Dun wheels could have been hunted by 63 gull pairs, considerably lower than the minimum of 104 hunting pairs suggested from data on the size and overlap of core

hunt areas.

Analyses above indicate that data on the influence of Puffin density and behaviour on hunting gulls is crucial for assessing how many Puffin easting gull pairs could hunt the island. Analyses to follow present such data.

2.5 HUNT SUCCESS, HUNT FREQUENCY AND NUMBERS OF FLYING PUFFINS

Hunts were significantly more likely to end in a kill when Puffin air numbers were low than when there were larger numbers in the air (χ^2 = 3.64 $P < 0.05$ 1-t) (Fig. 2.15). Data illustrated indicate that more than one in three hunts were successful when Puffin numbers were low, compared with one in five when numbers were moderate and one in fifteen when numbers were high.

Gulls had more encounters with Puffins per hunt minute when air numbers were low (Mann-Whitney U = 85, $P < 0.001$) (Fig. 2.16). There was no difference in the number of catches made per hunt with different Puffin air numbers (Mann-Whitney U $P > 0.1$ all comparisons) (Fig. 2.17). However, more catches were held and led to a kill with low numbers than under other conditions (χ^2 = 5.39, $P < 0.025$, 1-t) (Table 2.2).

Other aspects of hunting behaviour also varied with changes in Puffin numbers. There was significantly more agonism between flying gulls when Puffin numbers were low than when they were high (t = 2.041, $P < 0.05$ 1-t), but there was no difference in agonism in moderate and high number conditions (t = 0.64, NS $P > 0.05$ 1-t) (Fig. 2.18).

Gull patrol areas were similar in low and moderate Puffin numbers (t = 0.861 NS $P > 0.1$, 1-t), but hunts covered a signi-

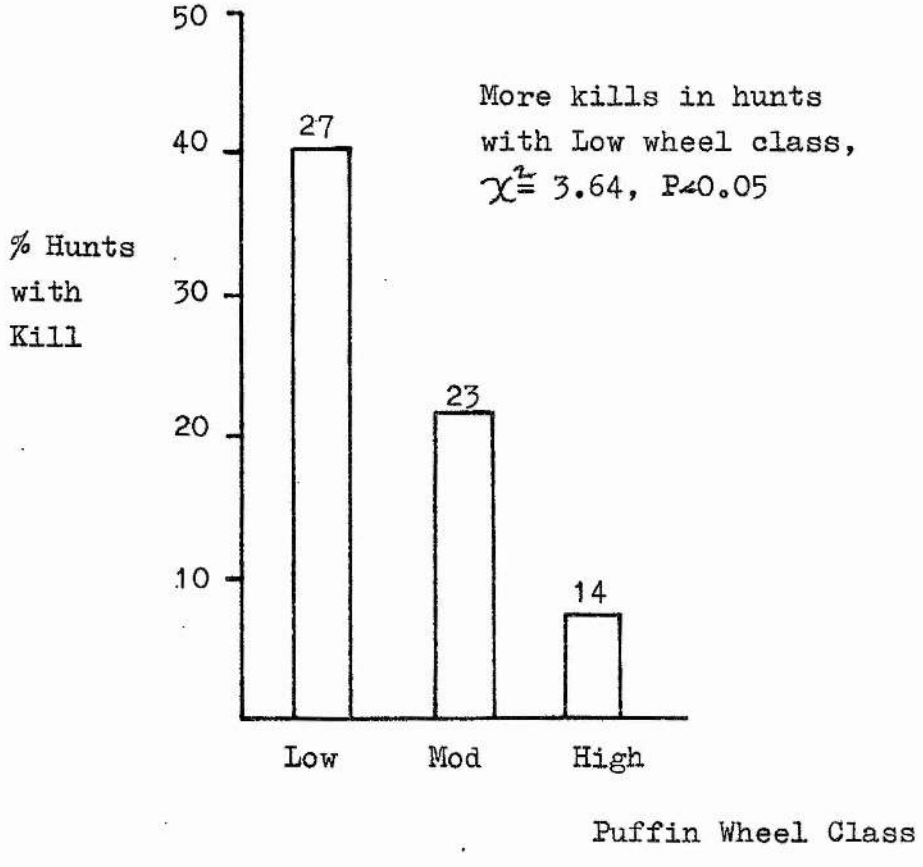


Fig. 2.15 % hunts leading to kill and Puffin wheel classification

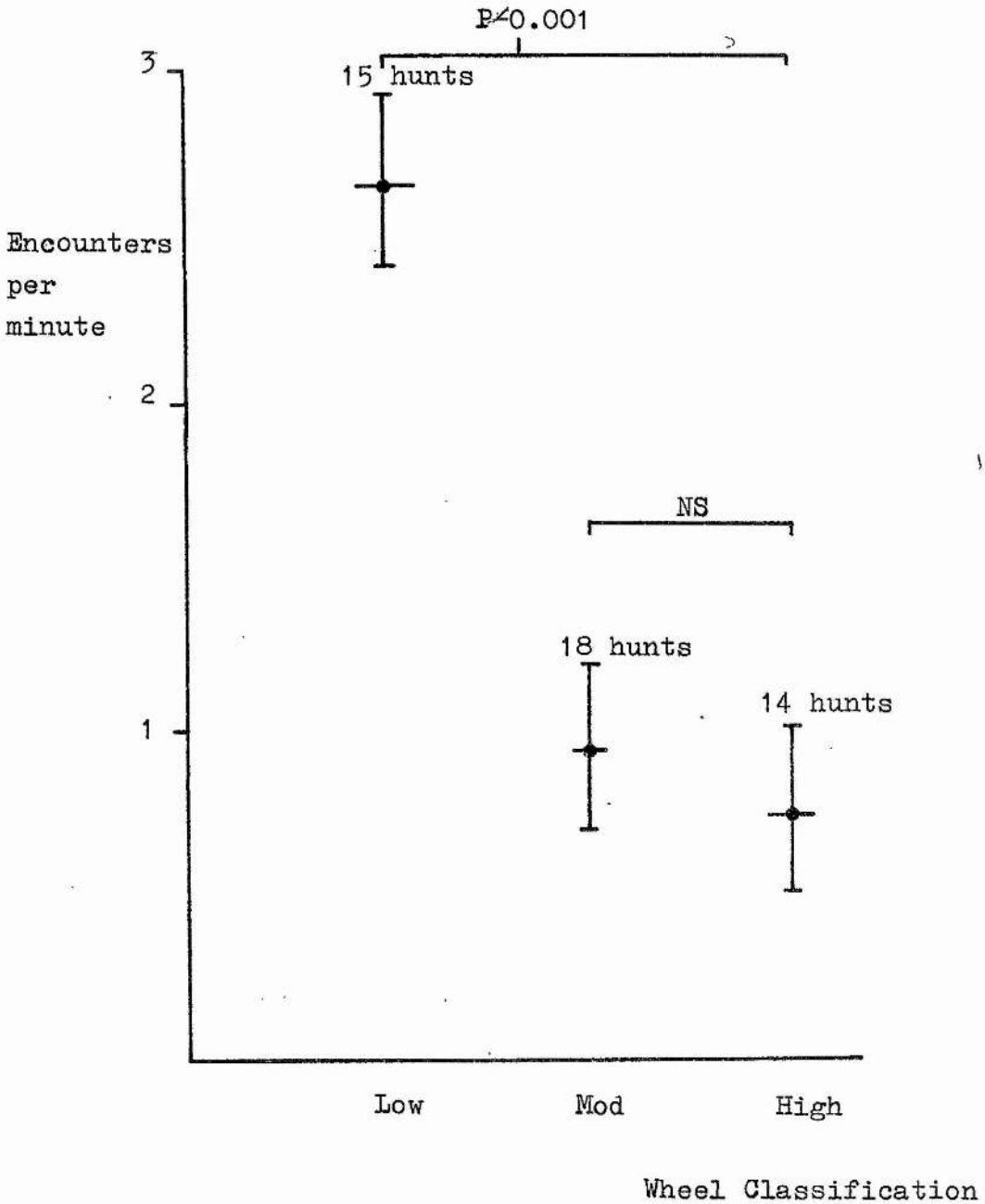


Fig. 2.16 Encounters per hunt minute and Puffin wheeling activity

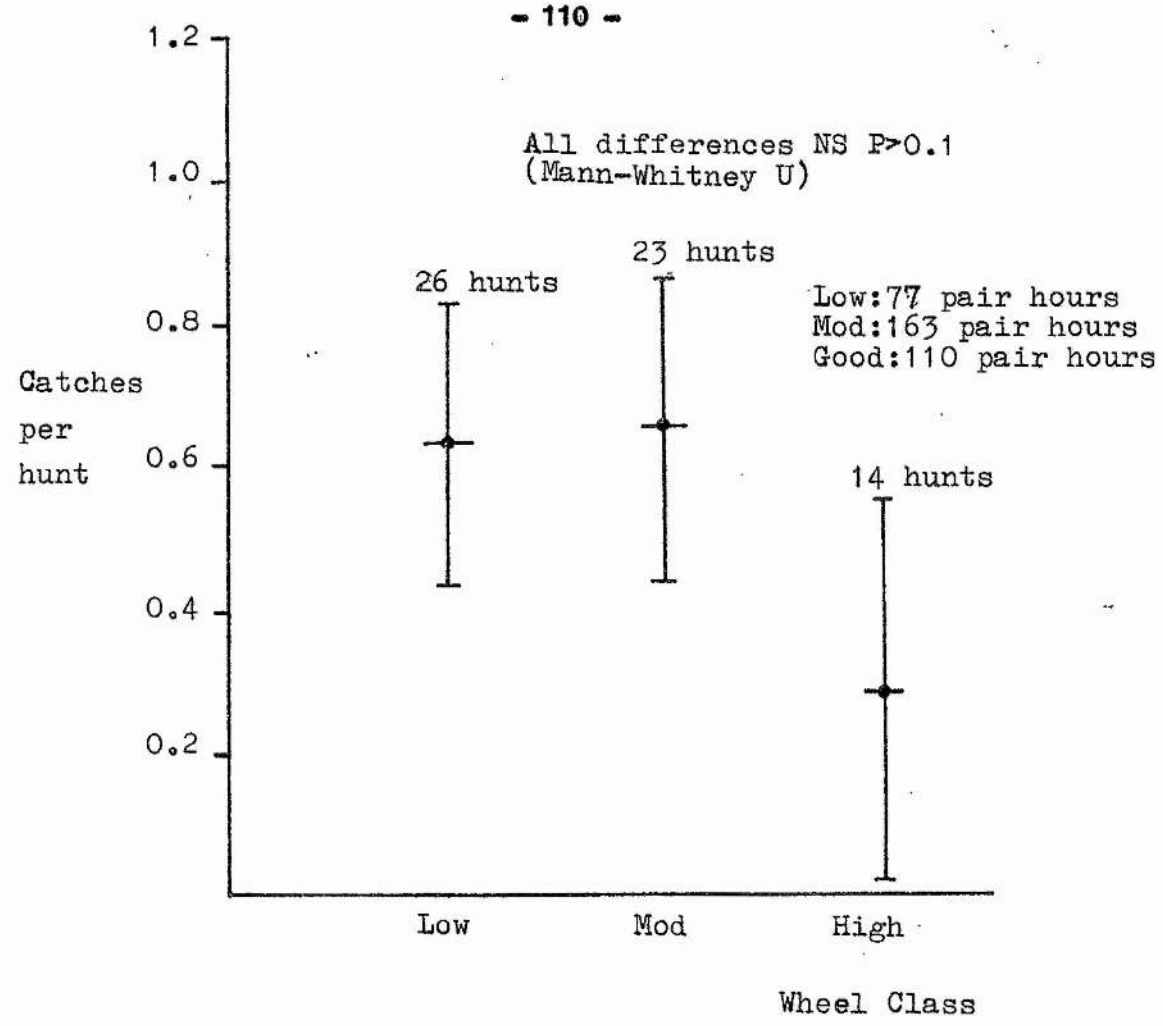


Fig. 2.17 Catches per hunt and Puffin wheeling activity

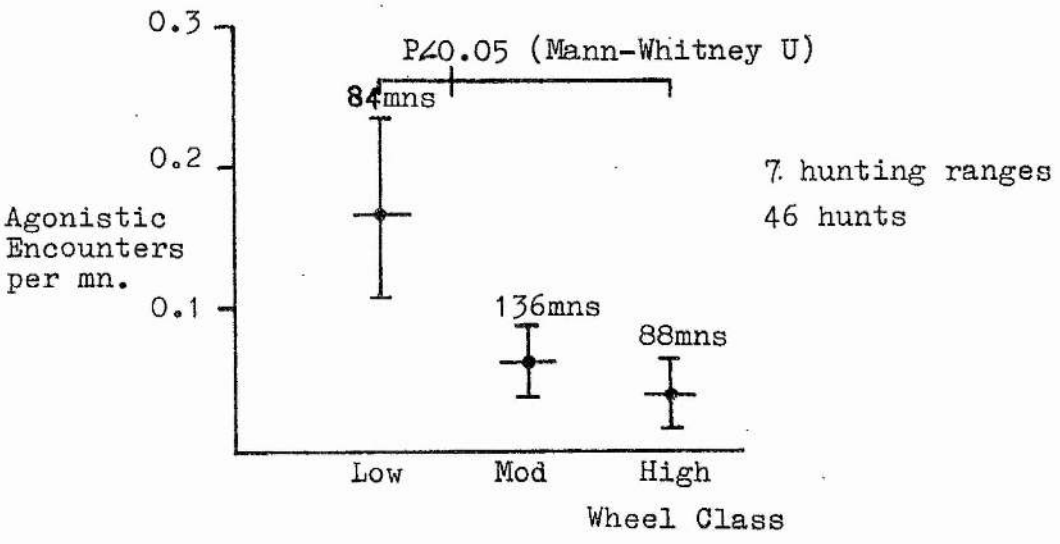


Fig. 2.18 Hunting gull agonism and Puffin wheeling activity

Table 2.2 Type of Catch/Puffin air action

Puffins/ Catch	Low	Moderate	High
Dropped	6	13	19
Held to kill	11	6	17
	17	19	36

Fewer catches dropped with lower Puffin numbers in the air $p < .025$ ($\chi^2 = 5.39$ 1-t)

ficantly larger area when Puffin numbers were high ($t = 2.07$, $p<0.05$ 1-t (Fig. 2.19).

Hunt durations were similar under all Puffin number conditions, most hunts lasting 12 to 14 minutes (Mann-Whitney $U p>0.1$ all comparisons) (Fig. 2.20).

The gulls' readiness to hunt seemed to reflect variations in hunt success described above. There were significantly fewer hunts per pair per hour under high to very high Puffin number conditions in the Dense study area than when numbers were lower (Mann-Whitney $U = 6$, $p<0.001$ 1-t) (Fig. 2.21). On average, one member of a Dense area pair hunted once every one and a half hours when Puffin numbers were low, and once every three hours when numbers were moderate. Hunting was reduced to one hunt per pair every six and a half hours when numbers were high, and to only one hunt every 250 hours when numbers were very high. In other words, when Puffin air numbers were very high gulls vitrually stopped hunting.

For pairs hunting the Sparse area during the full nestling period, there was a slight, but not significant, tendency for more frequent hunting when Puffin numbers were classed as high or very high relative to that area (Fig. 2.21). On average, one member of a Sparse area pair hunted once every five to six hours.

Discussion

The decline in hunt success with increasing numbers of Puffins in the air indicates that gulls may have been confused by large numbers of potential prey, as has been documented for a few other predators (e.g. Neill and Cullen 1974). Data on the declining number of encounters and increasing number of

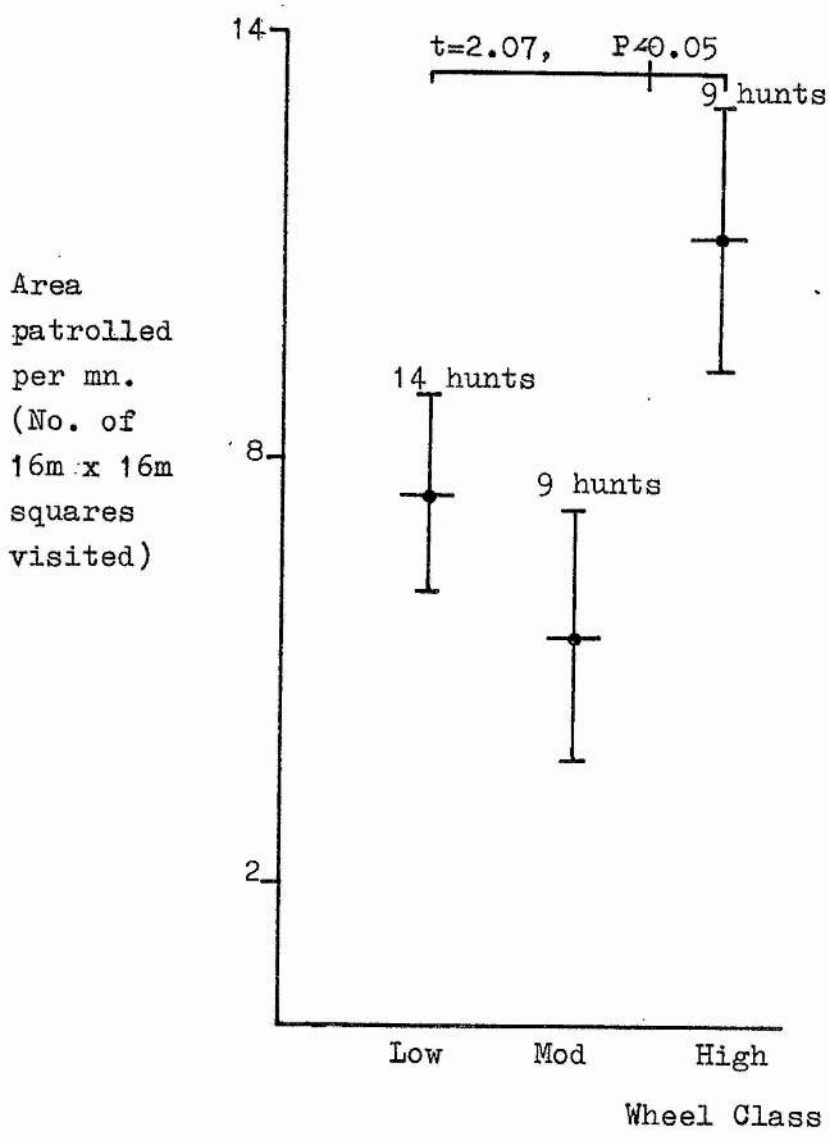


Fig. 2.19 Gull patrol area and Puffin wheeling activity

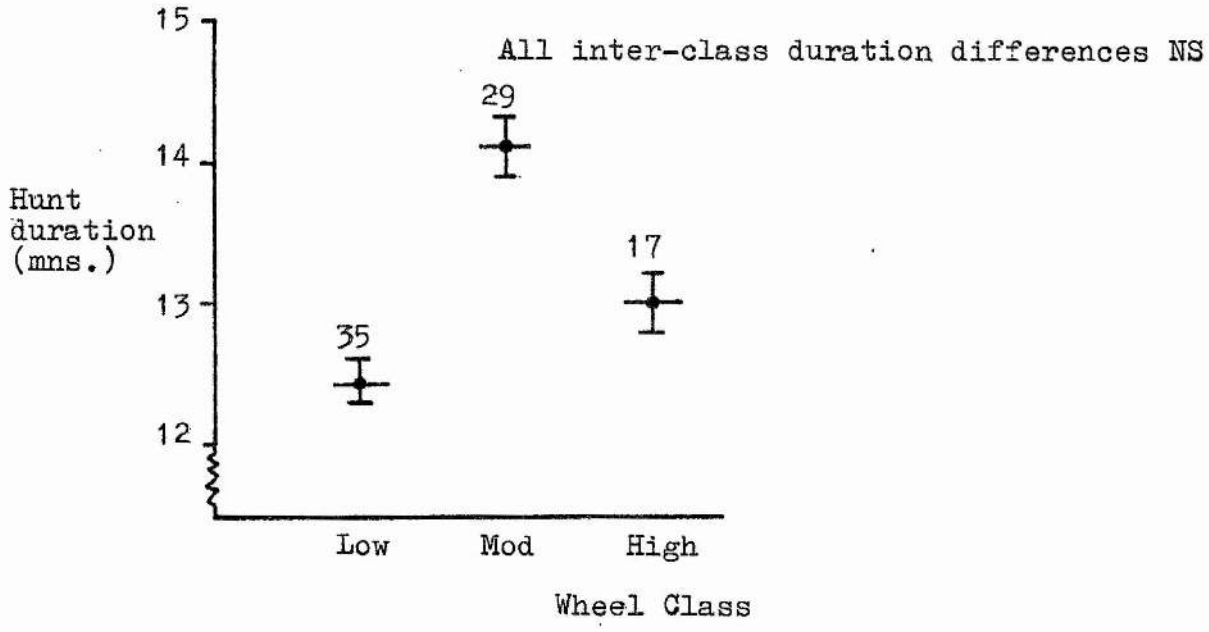


Fig. 2.20 Gull hunt duration and Puffin wheeling activity

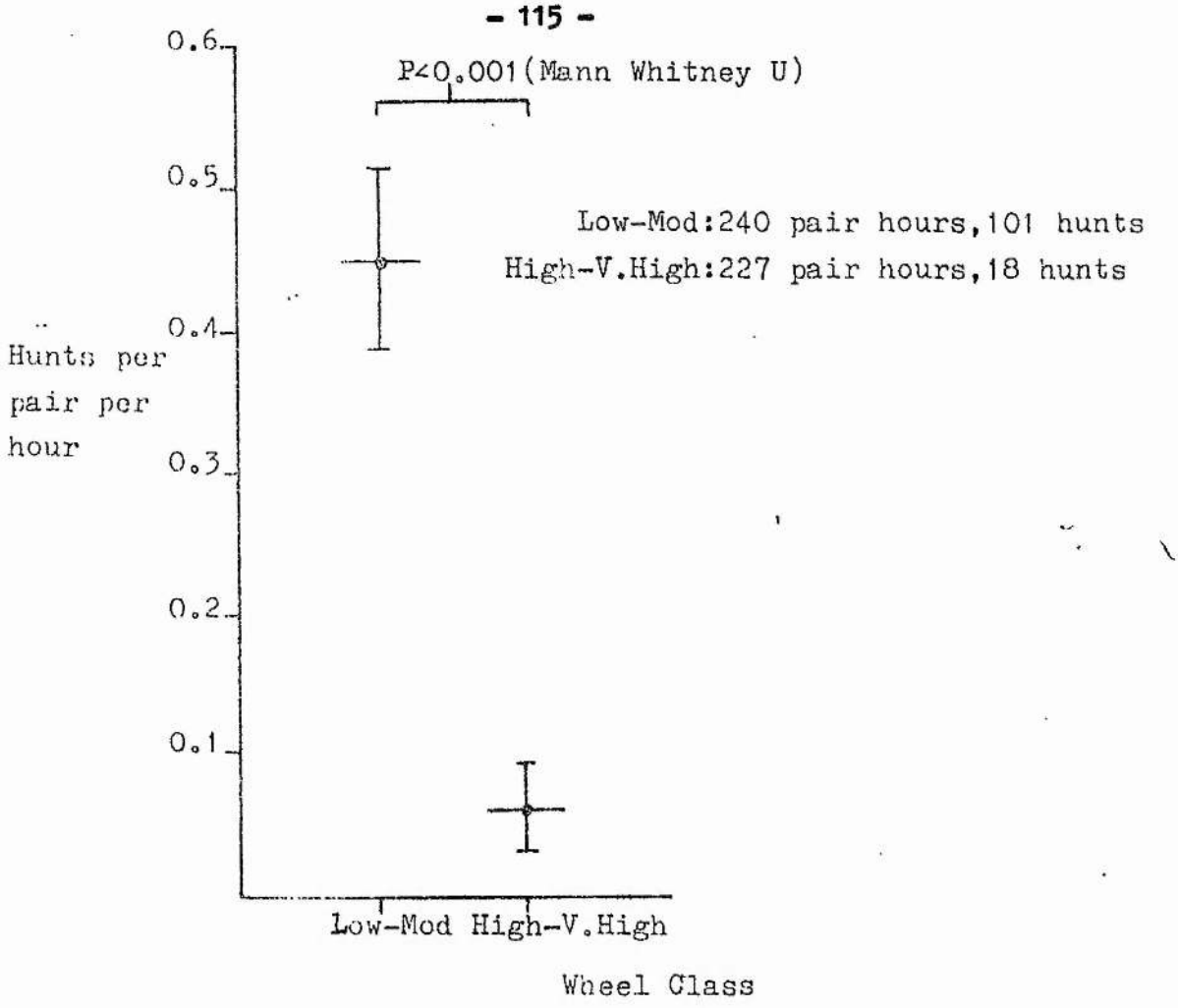


Fig. 2.21 **Gull** hunting frequency and Puffin wheeling activity. Nestling period, Dense Area

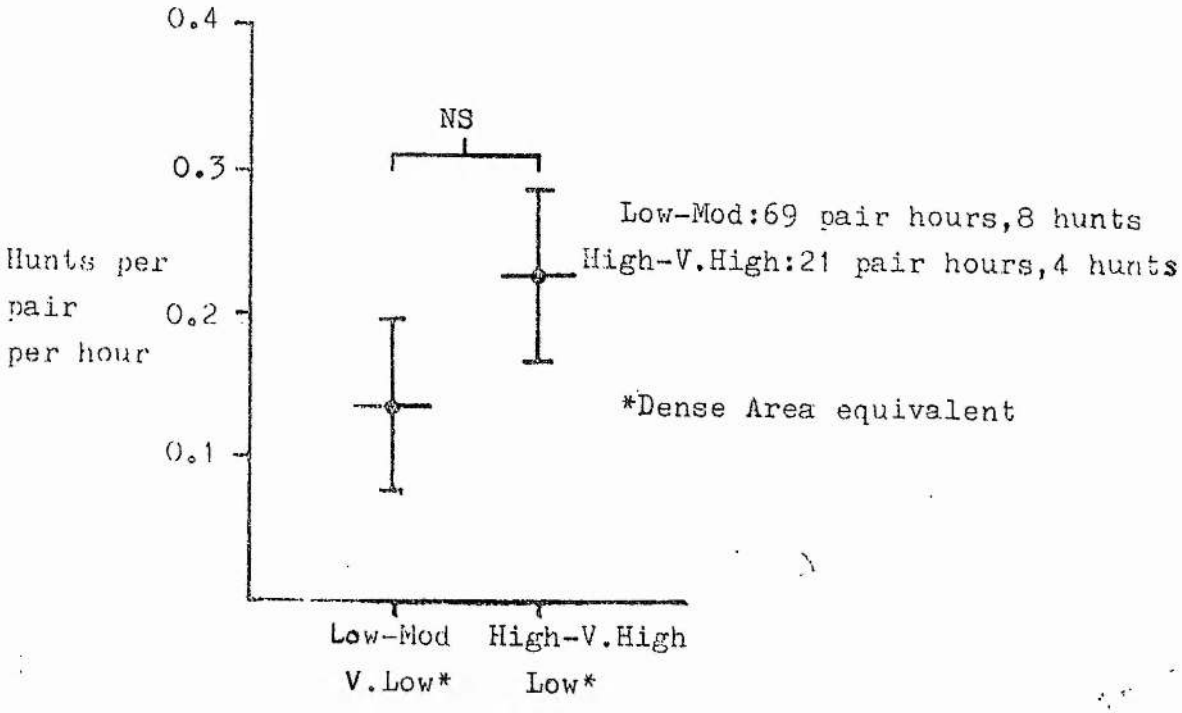


Fig. 2.22 Gull hunting frequency and Puffin wheeling activity. Nestling period, Sparse Area

dropped catches with higher air numbers strongly suggests such a confusion effect, implying that a gull's ability both to select and efficiently close on prey was impaired when large numbers of prey were in the air.

Changes in hunt frequency and agonism with changes in Puffin numbers suggest that gulls were able to discriminate differences in profitability of hunting under different Puffin number conditions and adjust their behaviour to maximise efficiency.

The low observed hunt frequencies in the Sparse area might mean that due to the generally low numbers of Puffins flying over this area gull hunting was very efficient and hence fewer hunts were needed to meet food requirements. Conversely, very low numbers of Puffins might make hunting in the Sparse area inefficient for long periods, again depressing hunt frequency. To assess these alternatives, gull hunting behaviour for several weeks during the nestling period was modelled for both Sparse and Dense areas.

2.6 MODELS OF GULL HUNTING IN DENSE AND SPARSE AREAS OF DUN

Aims

These models analyse how efficiently gulls partitioned their hunting time, given the influence of Puffin numbers on hunting success described above. They also assess the match between kills expected from known hunting frequencies/success rates and kills found at middens of known hunting pairs in the study areas. This assessment gives a means of judging how well the midden clearance technique described in Chapter One reflected the real extent of Puffin killing by individual gull pairs.

Lastly, they allow comparison of the hunting effort expended by pairs hunting in Dense and Sparse study areas to meet feeding requirements.

Methods

Data on daily Puffin number fluctuations, observed gull hunt frequencies and kill success rates were used as a basis for these models.

Classifications of Sparse and Dense Puffin numbers over 62 days between 17/5 and 22/7/77 indicate a significantly lower level of Puffin activity in the Sparse area ($\chi^2 = 14.13$, $P < 0.05$) (Table 2.3). Only 13% of days in the Sparse were classed as having high or very high Puffin numbers relative to that area, compared with 45% of days in the Dense. This assessment of Puffin attendance and air activity at the two areas agrees with quantitative comparisons of Puffin numbers made using time-lapse photography in 1975 (Harris 1980). In the time-lapse study, differences between the areas were highly significant in all study periods ($P < 0.001$), only 20% of Sparse area photographs having some birds present on the ground, compared with 85% of the Dense area photographs.

The models analyse gull hunting behaviour during part of the nestling period in June-July, during which gulls increase their Puffin killing. (See Chapter One.)

The models assume that gulls can hunt throughout the average 16 hours of daylight in the nestling period (taken from tables of sunrise and sunset times). The behaviour of Dense gulls is modelled for a 32 day period between 8/6 and 8/7/78 when all corpses found in the middens of six pairs

Table 2.3 Dun Puffin Action: 17/5/77 to 22/7/77

Area / Action	Sparse	Dense	
Low/ Moderate	54	34	88
High/ Very High	8	28	36
	62	62	124

Sparse action lower than Dense $p < 0.005$ ($\chi^2 = 14.13$)

hunting in the study area were collected. The expected kill for a single pair is taken to equal the observed average kill of 1.62 Puffins per pair per day at six middens during this period. The proportion of days having different Puffin air numbers from low to very high is calculated from Table 2.3. Expected hunts for any one Puffin air number condition are calculated using data on hunt success rates for that condition and by assuming that gulls hunt as much as is necessary to provide 1.62 Puffins per day.

Assumptions for the Sparse area model are as for the Dense model, except that hunts and kills are generated from data on kills at middens of six known Sparse hunt study area pairs for a 44 day period between 5/6 and 25/7/77. This model also assumes that Sparse hunt success is similar to Dense 'low' air number success, taken as 41% for all Sparse air number conditions.

Results

The Dense area model indicates that gulls did not divide their hunting effort in such a way as to provide the required average number of Puffins on any one day, regardless of Puffin air numbers (Table 2.4). Far more hunts occurred with low Puffin air numbers, and far fewer with high to very high numbers than would be expected if this was the case. This concentration of hunt effort in low to moderate Puffin number periods drastically reduced the overall number of hunts for the required kill over 32 days. Over four hundred hunts would be expected if gulls hunted to provide a fixed ration of 1.62 Puffins on any one day. Under 200 possible hunts could provide a roughly similar kill over the total 32

Table 2.4 Expected and observed hunting behaviour of single gull pairs with varying Puffin air numbers during gull nestling period

DENSE

Puffin air numbers	Low	Mod.	High	V.High	
Days	8.26	9.28	8.26	6.20	32
Hours available [1]	132.16	148.48	132.16	99.20	512
Hunts expected [2]	33	68	191	143 +	435+
Possible real hunts from obs. hunt frequency	87	49	20	1	157
Expected hunts/ pair/hour	0.25	0.46	1.45	1.44+	
Observed hunts/ pair/hour	0.66	0.33	0.15	0.004	
Expected kill [3]	13.38	15.03	13.38	10.04	52
Possible kill from obs. hunt frequency	36	11	1	-	48
Obs. kill at middens [4]					52

1. From observed daily number classifications 17/5 to 22/7/77 and assuming average 16 hours between sunrise and sunset for 32 days in June - July.

2. Hunts required for 1.62 kills per day [4], given hunt success rates observed as 41%. 22%, 7% and possibly ∠7% for low → v. high conditions respectively.

3. Assumes average pair requires 1.62 Puffins per day [4].

4. Mean value from clearance of middens known to be used by Dense study area pairs 8, 11, 12, 13, 14 and 15 over 32 days 8/6 to 8/7/78.

days on the basis of observed hunting behaviour. The shortfall of four Puffins in the possible kill resulting from observed hunting compared with the expected kill, is very small - equivalent to one Puffin too few per eight days. There is thus close agreement between the kill observed at middens and the possible kill from observed hunting behaviour. This lends support to some of the assumptions of the model described above, such as hunting being restricted to daylight hours. There is no support for the idea that gulls hunt to provide a fixed average Puffin ration on any one day. Rather, the model indicates that gulls were efficient at gauging the profitability of hunting under different Puffin number conditions, and hunted most when the chances of a quick kill were highest.

Expected and observed hunt frequencies for Sparse birds under different Puffin air number conditions show a close correspondence (Table 2.5). Again, this suggests that, as with Dense pairs, observed hunting behaviour of Sparse birds could have provided the observed number of Puffin prey at Sparse middens. The shortfall between possible and expected kill amounts to roughly one Puffin per pair per week, similar to the Dense area. This again gives a measure of how well the midden clearance technique reflected actual Puffin kills. There is no evidence from either model that midden clearance severely underestimated the probable real kill. For the Sparse area, the shortfall in kills could be met by a slight increase in hunt frequency for short periods. Given that Dense pairs hunted as often as once every one and a half hours, such an increase would be well within the capabilities of the species.

Table 2.5 SPARSE — Expected and observed hunting behaviour of single gull pairs with varying Puffin air numbers during gull nestling period

Puffin air numbers	Low → Mod.	High → V.High	
Days	38.28	5.72	44
Hours available [1]	612.48	91.52	704
Hunts expected [2]	123	18	141
Possible real hunts from obs. hunt frequency	104	21	125
Expected hunts / pair/hour	0.20	0.20	
Observed hunts / pair/hour	0.17	0.23	
Expected kill [3]	50.5	7.5	58
Possible kill from obs. hunt frequency	43	9	52
Obs. kill [4] at middens			58

1. From observed daily number classifications 17/5 to 22/7/77 and assuming average 16 hours between sunrise and sunset for 44 days in June - July.

2. Hunts required for 1.32 kills per day [4], assuming hunt success as for Dense 'low' classification of 41% for all Sparse air number conditions.

3. Assumes average pair requires 1.32 Puffins per day [4].

4. Mean value from clearance of middens known to be used by Sparse study area pairs 2, 4, 5, 6, 28 and 29 over 44 days 5/6 to 25/7/77.

Discussion

The slight increase in Sparse hunting activity during periods of relatively high Puffin air numbers, although not significant, suggests that hunting in this area might have been more efficient in such periods. This could have happened even if the gulls' catching ability was not affected by changes in Puffin air numbers. For example, under lower air number conditions gulls might have had to range over large areas in order to encounter potential prey. With increases in air numbers, more potential prey might have been encountered in a smaller area. Gulls would thus have had a higher energy return against energy expended while hunting during periods of higher air numbers over the Sparse area. Since 'high' numbers for the Sparse were equivalent to 'moderate' numbers for the Dense, this argument has limits, since it has already been shown that with high Puffin numbers relative to the Dense area, gulls hunting there ranged over a wider area than with lower relative numbers.

The models take no account of small scale variations in Puffin air numbers within days. Diurnal fluctuations in Puffin colony attendance are well documented (e.g. Lockley 1953, Myrberget 1959a). Attendance usually increases in the evening, with an obvious increase in wheeling activity. Such short term increases in Puffin air numbers could, on the basis of data and arguments presented here, have given birds hunting in the Sparse area time to hunt efficiently even within days whose overall air activity was classed as 'low'. For pairs hunting in the Dense area, such short term peaks in Puffin numbers would have made hunting more difficult.

Conversely, observations in 1976-78 showed that for long periods during many days, the Sparse area was almost devoid of Puffins. This could have made hunting more difficult for Sparse pairs. Pairs in the Dense area almost invariably had at least a few Puffins available even on days classed as 'low'.

There are thus in theory reasons why Sparse pairs might attempt to exploit the Dense area on occasions, and vice versa. Evidence from recoveries of Puffins ringed in the two areas and later recovered at middens indicates that Sparse pairs do hunt over the Dense area, but not vice versa (Harris 1980). 40 out of 80 recoveries of Puffins ringed in the Dense area were found away from that area, compared with two out of 42 birds ringed in the Sparse area being found away from the Sparse. Of these two, one was found at a gull roost on Hirta, the other in the midden used by pair 13, the pair mentioned earlier as being the only breeding gulls on Dun known to steal corpses from other pairs. These recoveries suggest that on balance, the difficulties of prey shortage experienced by Sparse pairs may be more acute than the difficulties of prey superabundance experienced by Dense pairs.

2.7 THE THEORETICAL RELATIONSHIP BETWEEN PUFFIN NUMBERS AND PREDATION

Differences in observed and probable hunting behaviour of gulls in the two Dun study areas with variations in Puffin air numbers give a means of describing the theoretical relationship between gull activity and Puffin numbers. This is shown diagrammatically in Fig. 2.23.

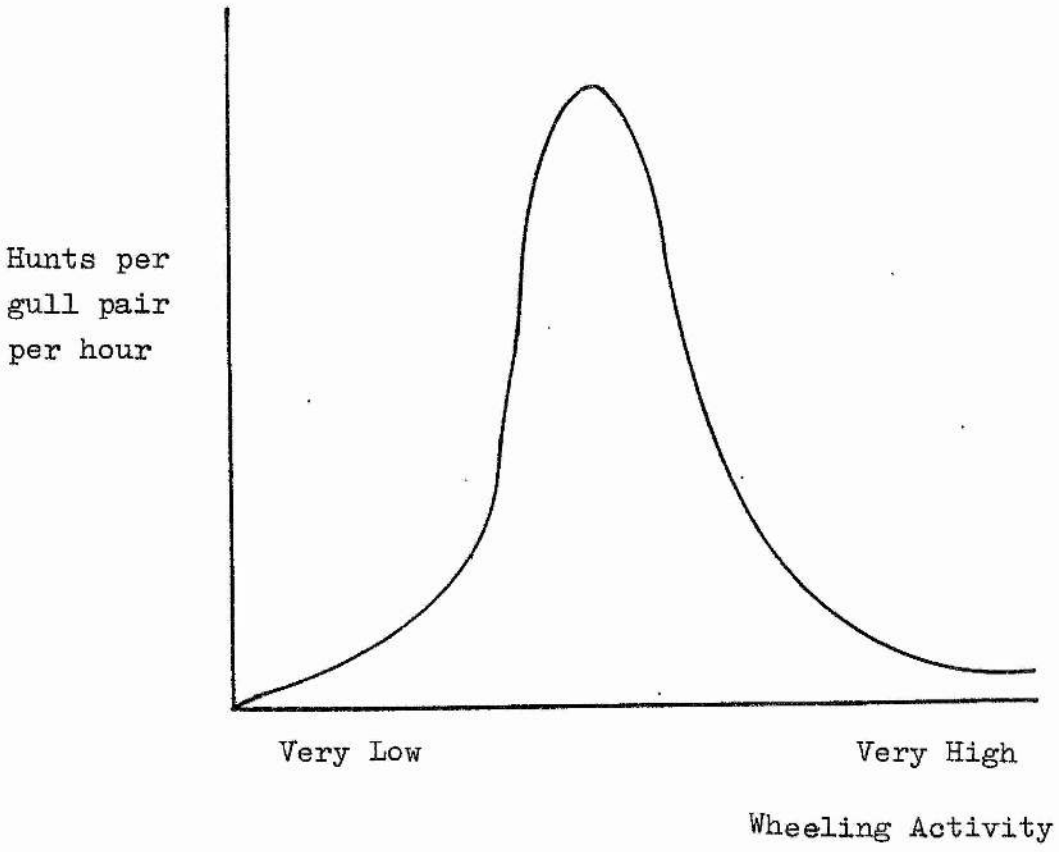


Fig. 2.23 Theoretical relationship between gull hunting frequency and Puffin wheeling activity

When Puffin numbers are very low there is likely to be little hunting activity because hunting is inefficient. As Puffin numbers increase, slightly more hunts should be expected. When Puffin numbers reach a level where hunting is most efficient - as expressed in terms of Puffins being both vulnerable to attack and easily accessible to gulls - there should be a sharp increase in hunt frequency. With greater numbers of Puffins, hunt success falls off sharply, and this should be reflected in a drastic reduction in hunt frequency. With the highest Puffin air numbers, gulls are least efficient at hunting and hunt frequency should tend towards zero.

This general relationship is meant to apply to both Sparse and Dense areas and to other Puffin colonies with specialist gull predators, although the actual hunting peak relative to numbers of Puffins in the air may vary. For instance, the observed Dense area hunting peak possibly occurred with higher Puffin numbers than the proposed Sparse area peak.

An individual Puffin's risk of being killed is not a simple inverse function of the number of other Puffins present at the colony at that time (Fig. 2.24). If as proposed in Fig. 2.23 gull hunt frequency initially increases as a nearly linear function of increasing Puffin numbers, an individual Puffin's predation risk will at this stage be roughly constant. Once Puffin numbers reach a level which allows the most efficient hunting by gulls, the risk of being killed will increase due to the sharp increase in hunt frequency. With the highest Puffin numbers, kill risk for

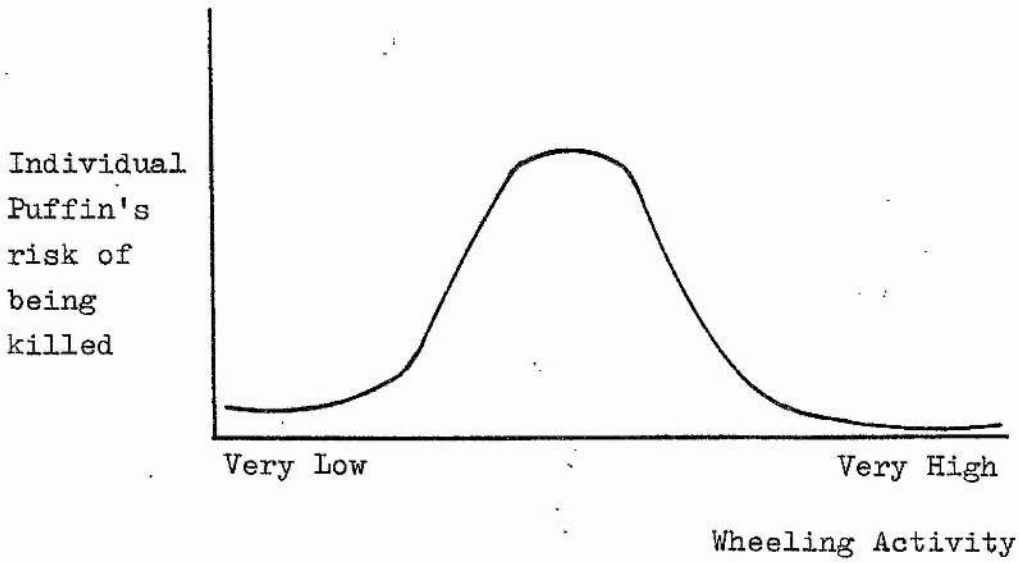


Fig. 2.24 Theoretical kill risk for an individual Puffin with variations in wheeling activity

an individual Puffin will tend towards zero, being a function of decreasing hunt frequency, decreasing hunt success, and increasing numbers of other potential Puffin prey.

Discussion

Although a gull's ability to catch Puffins is adversely affected by very high concentrations of prey, day to day variations in Puffin colony attendance may make this difficulty less acute than having too few prey accessible in a hunting area. Although diurnal peaks in attendance at low burrow density sites may increase hunting efficiency, this benefit would be reduced if there was increased competition for hunting space at such times. It is possible that some gulls nesting in the Sparse area which successfully raised young on a diet of Puffins were able to do so only by having occasional access to the higher prey densities over the Dense area. The effects of prey numbers throughout the breeding season, and of gull competition for hunting space on the hunting behaviour of Sparse area gulls cannot be fully determined from the Dun data to date. A gull removal experiment in the Sparse area, backed up with further Puffin ring recoveries at middens, or radiotelemetry of hunting gulls, would help separate the effects of these variables and suggest whether the Sparse area alone could support successfully breeding, Puffin eating, gulls.

At present it is suggested that Puffin colonies with a low burrow density, less than or equal to the Dun Sparse area and/or having a small overall number of breeding Puffins, may not represent a suitable feeding area for

predatory gulls throughout the breeding season. Gull predation at such sites should be occasional and opportunistic. Colonies with higher burrow density, perhaps greater than the Dun Sparse area and equal to or greater than the Dun Dense area provide a food source which gulls could feasibly exploit throughout a breeding season. The number of gull pairs able to exploit such a colony will in part be limited by inter-gull competition for hunting space, so that for example, the number of pairs able to exploit a high burrow density colony of a similar size to Dun will be of the order of tens, rather than hundreds. The lack of regular predation by gulls at many British Puffin colonies, for example large colonies in east Britain, is thus surprising. Human predation on gulls has undoubtedly influenced the present British distribution of L. marinus. Availability of other good and abundant food sources, such as Sandeel prey or waste from trawlers and at rubbish tips, may also allow large numbers of gulls to nest in a small area, such as on North Rona. Such large numbers breeding in a small area might interfere with Puffin hunting by a smaller number of pairs which could theoretically subsist on Puffins in that area. This could reduce the number of pairs expected to be specialised Puffin killers at a high burrow density site. Gull diet, hunting behaviour and breeding success on North Rona merits close study to investigate these questions.

For the Puffin, data presented here on the hunting behaviour of one of its avian predators suggests that an individual Puffin's risk of being killed is a complex function of Puffin numbers at the colony. A Puffin visiting

a colony in the virtual absence of other Puffins, such as might happen at colonies with very low burrow density, has only a slight risk of predation. With a higher number of other Puffins simultaneously present, such as might be unavoidable due to the traffic of birds feeding young and the presence of non-breeders at a high burrow density colony, predation risk may be high. With greater numbers of Puffins simultaneously present, predation risk for individual Puffins is slight. There could thus be selective pressure through predation for Puffins to synchronise their colony visits with as many other Puffins as is necessary to 'swamp' an aerial predator. Synchronisation with too few other Puffins could merely increase an individual bird's risk of being killed. For Puffins breeding in the Sparse area, sufficiently marked synchronisation of attendance is probably seldom feasible, due to the low overall number of birds breeding in that area. Most 'peaks' in Puffin attendance at that area merely serve to increase gull hunting activity, and increase a Sparse area Puffin's risk of predation.

Puffins breeding in the Sparse area are four to five times more likely to be killed by a gull than those breeding in the Dense area (Harris 1980). Estimates of the breeding populations at the two ringing sites used in this recovery study indicate that about two and a half times more Puffins bred in the Dense ringing area than in the Sparse area. Kill risk is thus not simply inversely proportional to the number of Puffins breeding in a local area. This adds to the complexity of gull influence on Puffins when considered

together with data presented here which show that kill risk for an individual Puffin is also not inversely proportional to the number of Puffins flying during hunt periods.

2.8 GENERAL DISCUSSION Links between the present study and studies of other vertebrate predators.

Hunting behaviour

There are few descriptions of the hunting behaviour of Puffin predators other than L. marinus. Collett (1921) states that a pair of White-tailed Eagles (Haliaeetus albicilla) which bred on the Norwegian island of Lovunden lived almost exclusively on Puffins which they caught in flight or took from the sea. Myrberget (1957) gives a full description of Puffin hunting by White-tailed Eagles in Helgeland, Norway, translated here to give a comparison with the behaviour of gulls on Dun. Myrberget says that: 'When an eagle comes in over the colony, all the Puffins take off or seek shelter. The eagle flies around the large flocks, while the Puffins don't bother the least. I've only once seen an eagle take a Puffin in flight. The Puffin was coming rapidly down a narrow valley when the eagle glided in front of the valley mouth, and the Puffin had neither time nor room to escape. Eagles often hunt Puffins in the big flocks which sit under the Alkebukta cliffs in summer. The Puffins dive when they come too close. The eagle's only chance is the moment when the Puffin surfaces, but it seldom makes a catch.' White-tailed Eagles at this site thus hunted Puffins more widely around the colony than was usual for gulls on Dun, but the Puffins' reaction to them at the colony was similar to that observed in Dun Puffins.

Although Peregrines (Falco peregrinus) and Gyr falcons (F. rusticolus) prey on Puffins in many areas (e.g. references in Myrberget 1959 b, Ratcliffe 1980), I have not been able

to find any descriptions of their Puffin hunting behaviour.

The form of hunting behaviour in gulls preying on Puffins is similar to that described for some raptors feeding on other prey. Peregrines use look-out points before hunting, and may circle high in the air before stooping on flying prey, a behaviour known as 'waiting on' (Treleaven 1977). Hunting Sparrowhawks (Accipiter nisus) may also use an ascending spiral 'prospecting flight' (Owen 1932, Pounds 1936).

Capture of Puffins at burrows, mentioned as a hunting method used by Kildan gulls (Williamson 1958) and by gulls at other localities (Lowe 1913, Lockley 1953) is similar to the hunting behaviour of a number of raptors which eat burrow dwelling prey. The Long-legged Buzzard (Buteo rufinus), Upland Buzzard (B. hemilasius), Greater Spotted Eagle (Aquila clanga), Steppe Eagle (A. rapax), Merlin (F. columbarius) and Saker (F. cherrug) catch rodents in this manner (Dementiev and Gladkov 1966).

Pairs of gulls have been seen hunting 'co-operatively' at other localities. Two gulls made a combined attack on a flock of Puffins on the water off Skokholm then shared the kill (Lockley 1953, p. 108). Among other seabird predators, Great Skuas (Catharacta skua) often work in couples while hunting or killing birds such as adult Kittiwakes (Perry 1948, Meinertzhagen 1959, Bayes et al 1964) as do Arctic skuas (Stercorarius parasiticus) hunting birds and rodents (Maher 1974, Anderson and Götmark 1980). Among raptors, combined aerial hunts of avian prey by two birds, sometimes a known pair, occur mainly in members of the

Falconidae, Merlins, Aplomada Falcons (F. femoralis) and Peregrine Falcons hunt jointly even outside the breeding season (St. John 1882, Meinertzhagen 1959, Dementiev and Gladkov 1966, Brown and Amadon 1968, Treleaven 1977), while Red-headed Falcons (F. chicquera) are 'often' seen hunting in pairs during the breeding season (Brown and Amadon 1968). Groups of crows (Corvidae) have been seen working together in kleptoparasitic attacks and in egg predation (Goodwin 1976). While Goodwin felt that this does not represent true co-operation, Montevecchi (1976) considered that individual crows probably benefit from hunting in pairs or groups. Corvid group foraging is not strictly analagous to hunting seen in gulls.

In carniverous mammals, joint or pack hunting occurs more frequently in the Canidae than in other families (Wilson 1975). For example, wolves (Canis lupus) have been seen driving caribou towards other members of the pack lying in wait (Murie 1944, Kelsall 1968), and in attacks on Wildebeest (Connochaetes taurinus) calves a second hyena (Crocuta crocuta) can counter the attacks of the mother, enabling the first to capture the offspring (Kruuk 1972). Co-operative hunting in canids differs from gull hunting in that, for example, wild dog (Lycaon pictus) packs can kill larger prey than single dogs (Schaller 1972). Wilson (1975) considered that such co-operative hunting behaviour may have evolved partly because canids, unlike most cats and other carniverous mammals, chase prey in the open, an idea relevant to the behaviour of gulls and falcons described here.

In some predator species, joint or communal hunts can

break down the group defences of prey, leading to individual prey becoming isolated, these isolated individuals being preferentially attacked (e.g. Estes and Goddard 1967, Dill 1978). In gull joint hunts the situation was somewhat different, with one member of a pair acting as a 'beater' for the other partner (cf Curio 1976), reminiscent of interspecific associations such as those where Ant-birds (Formicariidae) exploit anthropod prey flushed by marching swarms of army ants (Willis 1967).

Gull agonism in flight was ritualised in form and involved no overt aggression such as pecking, unlike aerial disputes in Herring Gulls (L. argentatus) (e.g. Tinbergen 1953). Ritualised aerial agonism is a regular feature of display in Accipiters and some Eagles (Brown and Amadon 1968). Beebe (1960) noted that there was 'an apparent lack of aggressive behaviour' between pairs of Peregrines feeding on alcids in the North-west Pacific, even although as many as five pairs at times hunted simultaneously in a small area, and invasion of one another's 'territory' was 'commonplace'.

Many features of the behaviour of hunting gulls, considered to be 'generalist' feeders, thus parallel hunting methods used by other, often more specialist feeding vertebrate predators. Constraints on hunting success, such as the anti-predator behaviour of bird flocks attacked by gulls or raptors, may have led to a convergence in hunting styles in these widely different groups.

Hunting ranges

Vertebrate territoriality has been the subject of numerous studies (references in Wilson 1975). The dis-

persion of living organisms is usually in part a response to other organisms, often conspecifics. Using data on the spatial distribution of animals ranging from unicellar organisms (Protista) to humans, Taylor et al (1978) state that 'with very few exceptions, randomness only occurs when density is so low that the one individual that can be found has no others with which to respond'.

Descriptions of how observed spacing patterns may be maintained through 'defence' of a territorial or 'exclusive area' (Noble 1939, Schoener 1968) have led to disputes about the generality or anthropormorphism of such definitions (e.g. Emlen, J.T. 1957, Willis 1967, Willis and Oniki 1978, Kaufmann 1971, Emlen, J.M. 1973). 'Working' definitions of territory are now normal, such as Davies' (1978) recognition of a territory 'whenever individual animals or groups are spaced out more than would be expected from a random occupation of suitable habitats'. Arguments about definitions, which have a bearing on determining the functions of territoriality, need not cloud data from field studies. A number of general findings from studies of vertebrate spacing and ranging behaviour can be outlined here to aid discussion of gull behaviour.

Avian territorial systems have been classified by Nice (1941). Studies of avian groups, such as raptors, indicate that the size of a bird's range usually represents the area the bird needs to cover to obtain enough food (Newton 1979). Reviews and mathematical models of spacing behaviour suggest that if food is uniformly distributed, individuals should tend to space themselves out, with each foraging near its

nest (Crook 1965, Horn 1968, Smith 1968, Brown and Orians 1970). In Arctic Skuas (Stercorarius parasiticus), pairs breeding colonially forage far from the nest, at sea, and eat mainly marine food, whereas solitary pairs defend feeding territories around the nest and eat mainly terrestrial food such as birds and rodents (Anderson and Götmark 1980). Differences in nesting distribution between the fringilline and cardueline finches are associated with differences in feeding habits. Fringillines rear their young on insects and spread themselves fairly evenly through the habitat. Carduelines feed their young primarily on seeds and nest in loose colonies, foraging away from the colony in flocks (Newton 1972).

Territorial defence of large areas by birds is considered by some to have evolved in response to competition for food (Stenger 1958, Pitelka (in Brown 1964)). This view is opposed by Lack 1954) on the basis of data which show that in Thrushes (Turdidae) most nestling and fledgling mortality may be ultimately attributed to predation, this leading to selection for spacing out of nest sites. However, Lack (1967) felt that the nesting dispersion of L. marinus in Britain was presumably related to food supplies.

In rodents, defended core areas seem to occur in situations where food is evenly distributed and dependable, but not otherwise (Emlen 1973).

If animals concentrate their activities in a core area within the home range, the extent to which this area is defended can vary between and within species in a continuum from exclusive use of an area to complete overlap with the

ranges of other animals (Emlen 1973). Discussing avian territoriality Brown (1964) introduced the concept of 'economic defendability', considering that birds should only be expected to defend a territory if there will be a net benefit in terms of fitness (although he did not use this term) from doing so. In such a scheme, there are costs and benefits to territoriality. For gulls on Dun, one benefit of defending a core hunting area in the vicinity of a Puffin wheel is access to prey. The cost of defending a larger area containing more wheels could set an upper limit to the size of a core area.

Even if there is spatial overlap of core areas, conflict between animals from neighbouring ranges can be avoided by neighbours using the same space at different times. Whether an animal defends an area at all times may be influenced by considerations of, for example, the rate of depletion and renewal of food resources in a foraging patch (see discussion of Optimal Foraging below). A gull hunting in its core area on Dun tended to defend that area while it was hunting, but not otherwise.

Retreat of neighbouring gulls without any conflict when attacked by 'owners' of core areas is reminiscent of agonistic behaviour in many other species (e.g. see Davies 1978). For example, Schaller (1972) comments that in disputes between lions (Panthera leo) in a pride area 'intruders were not chased to the border of the pride area, yet the attack induced ... the same effect as if they had been fully evicted'. Such behaviour suggests the 'Dear Enemy Phenomenon', recognised in principle for birds by Fisher (1954)

(and see Wilson 1975), where it should pay territorial individuals to recognise territorial neighbours, and waste as little energy as possible in hostile exchanges. Also, once the breeding season is well under way, a core area owner may stand to gain more in terms of fitness from fighting over that hunting space than an intruder. Such an asymmetry in expected pay-off to the contestants in a fight could lead to the ritualisation of contests, where the intruder retreats without a serious fight (cf. Maynard Smith and Price 1973).

Home ranges of Dun gulls overlapped widely. Except in some Buteo, Aquila and Elanus populations this is also the usual pattern in raptors (Newton 1979). Puffins on Dun constitute an abundant food supply for gulls. Gull ranging behaviour and defence of hunting areas is similar to that observed in a wide variety of predators exploiting abundant prey, and proposed in recent theories for animals exploiting evenly distributed food resources.

Hunt Success

The percentage of all attacks which lead to a kill have been determined for only a few species of raptors, and there are different opinions about interpreting data for some species. Low attack success ratios in strikes at birds, such as 7.5% and 5% determined by Rudebeck (1951) for European Peregrine Falcons and Merlins respectively, were considered by Brown (1976) to be too low due to the idea that many 'so-called attacks are not real attacks'. For example, a Golden Eagle may use 'fake' attack movements to

frighten prey into a vulnerable position (Hamerstrom 1970). Conversely, Parker (1979) felt that all Peregrine attacks he observed were genuine attempts to catch prey. Parker observed success ratios of 17% and 15% for male and female Peregrines preying on Feral Pigeons (Columba livia) at a Welsh coastal eyrie. Treleaven (1977) suggested a 25% success ratio for Peregrines preying on pigeons in Cornwall. In general it appears that wild raptors make more unsuccessful attacks than successful (Brown and Amadon 1968). Success ratios vary widely between species, possibly reflecting differences in the type of prey. Ospreys (Pandion haliaetus), which are fish predators, have observed success ratios of 80 to 90%, the highest known for any raptor (Lambert 1943, Ueoka and Koplin 1973). American Kestrels (F. sparverius) feeding mainly on insects, had a 51% success ratio, success varying with different hunting methods (Collopy 1973). Ferruginous Hawks (B. regalis) secured prey in 16.6% of attempted strikes at rodents, success again varying with hunting method (Wakeley 1978). The attack success of a female Merlin preying on waders (mainly Calidris spp.) in an American study varied with prey flock size (Page and Whitacre 1975). 25% of attacks on singletons were successful, compared with less than ten percent with flocks of 2 - 49 birds and 21.4% with larger flocks. Also, as shorebirds decreased in number during the winter, the Merlin's success rate declined, indicating that the availability of prey may also have affected its success rate. For wild raptors preying on birds, recorded success ratios thus range from five to 26%.

Reviewing carnivore data Schaller (1972) felt that a

predator's hunting success reflects the anti-predator behaviour patterns of prey species. For example, once a lion has started an attack chase, its chance of catching prey varies from 13 to 14% with reedbuck (Redunca redunca) or topi (Damaliscus korrigum) to 47% with warthog (Placochoerus aethiopicus). Schaller considered that comparison of the hunt success of different predators is difficult due to differences in prey capture technique, anti-predator behaviour of prey and seasonal variations in ecological conditions.

The success ratio of Dun gulls ranged from 0.72% to 1.64% with varying numbers of prey in the air. This is an order of magnitude lower than raptor success, even allowing that my data were more detailed than previous workers, and that I was probably scoring even some slight intention movements as attacks. Since gull predation on Dun Puffins is an example of local opportunism by members of a generalist scavenging and predatory species, it is perhaps not surprising that the predatory efficiency of gulls attacking birds is less than in a species such as the Peregrine, a specialist avian predator morphologically adapted for high speed aerial attacks.

That gulls succeeded in capturing sufficient prey through relatively inefficient hunting by comparison with raptors may indicate how certain features of the prey, such as prey availability, could result in differences in hunting efficiency between different types of avian predators. For example, studies of Peregrines discussed here have mainly been based on observations of attacks on pigeon flocks.

Such flocks are transient, and may be unpredictable in time and space, placing a premium on a quick kill for the pigeon predator. Puffin wheels on Dun are prolonged in time and spatially predictable. There may thus be little selection pressure for more efficient hunting in gulls exploiting flying Puffins in wheels.

Confusion Effect

Data on Merlin predation of wintering waders (Page and Whitacre 1975) indicates that prey numbers may influence hunt success. The finding that Merlin attacks on large flocks were more successful than attacks on small flocks may indicate that individual prey were themselves impeded in escaping by large numbers of conspecifics in the vicinity, as in Schaller's (1972) interpretation of lion attacks on large ungulate herds.

Evidence from the Merlin study does not suggest that Merlins were 'confused' by large numbers of prey, but interpretation of variations in attack success with varying numbers of prey is hampered by not knowing the condition of waders in flocks of different sizes. Birds in small flocks could have fed less than those in larger flocks, their poor condition making them more vulnerable to the predator. There is evidence from studies of a wide variety of predators that animals which are in poor condition have a higher risk of predation than healthy prey (e.g. Murie 1944, Van Dobben 1952, Mech 1966, Kruuk 1970, 1972, Schaller 1972). There is no data on the condition of Puffins in different sizes of wheels. During most of the day, a wheel contained a mixture of adult and sub-adult Puffins. It is thus unlikely

that the effect of prey number is confounded with possible effects of prey condition in the gull study.

In a study of Goshawk (Accipiter nisus) predation on pigeons, attacks on singletons and small flocks were more successful than attacks on flocks of more than ten pigeons (Kenward 1978). This was partly because singletons were in poor condition and partly because the hawk achieved less surprise as flock size increased.

Other studies have shown that predators are detected more quickly by larger groups of birds (Powell 1974, Siegfried and Underhill 1975, Hoogland and Sherman 1976). In some animals, such as some species of primates and rodents, there is even 'division of labour' within groups, with members of some age-sex classes spending more time on the alert for predators than others (Bertram 1978). Grouping by feeding Ostriches (Struthio carnelus) decreases an individual bird's vulnerability to predation due to the temporal patterning of vigilant head raising by group members (Bertram 1980).

These studies, and models of predator avoidance in avian groups, such as those of Pulliam (1973) and Stinson (1980), describe the behaviour of birds in foraging flocks which are subject to attack from predators relying on surprise for a successful kill. This is completely different from interactions between gulls and Puffins, where neither predator nor prey is concealed.

The most useful comparative data for assessment of gull-Puffin interactions comes from studies of predation on fish schools and swarms of aquatic invertebrates. The resemblance between fish schools and flocks of birds such as

Dunlin (Calidris alpina) and Starling (Sturnus vulgaris) flocks has been commented on by other observers (Major and Dill 1978).

There are many similarities between Puffin wheels and fish schools. Schooling is a highly eclectic phenomenon (see Shaw 1962), but some general features of schools can be outlined. Radakov (1973) defines a fish school as a 'temporary group of individuals, usually of the same species, all or most of which are in the same phase of the life cycle, actively maintain mutual contact, and manifest, or may manifest at any moment, organised actions which are as a rule biologically useful for all members of the group'. While schooling may lead to a patchy distribution of prey and thus be a form of concealment (Brock and Riffenburgh 1960, Cushing and Jones 1968, Olson 1964, Treisman 1975), once a school is detected there is often little or no habitat cover for predator or prey. This also applies to aquatic invertebrate swarms. Predators attacking fish schools usually make repeated kill attempts. Predator-prey interactions in this system are thus in many ways analagous to gull-Puffin interactions.

That large numbers of grouped prey may 'confuse' a predator by dividing its attention among a number of possible prey and making selection of a single prey difficult (cf. Allen 1920, Miller 1922) was first demonstrated experimentally in Goldfish feeding on Daphnia (Daphnia daphnia) swarms (Welty 1934). The food intake of the Goldfish was less with swarms of high density than with moderate density, due to a depression of the fishes' capture rate, itself a

function of increasingly inappropriate attack behaviour in the fish. Sticklebacks (Gasterosteus aculeatus) attacked straying individual Daphnia in preference to swarms (Milinski and Curio 1975, Milinski 1977). Cod (Gadus morhua) took longer to catch single pollack (Pollachius virens) from a school than to catch isolated fish (Radakov 1958). The success ratio of squid (Loligo vulgaris), cuttlefish (Sepia officinalis), pike (Esox lucius) and perch (Perca fluviatilis) attacks on small fish declined with increasing prey school size (Neill and Cullen 1974). For perch, the only chasing predator in the Neill and Cullen study, shoals seemed to disrupt attacks by 'forcing the predator continually to switch targets during his pursuit'.

Confusion in the predator could have a number of causes. A predator's attention may be diverted from one prey to another during attack, as suggested from the fish predator studies. Erratic movements (termed protean behaviour by Driver and Humphries 1970) by individuals in a group, such as occur in some fish schools under attack (Eibl-Eibesfeldt 1962) and in Dunlin (Calidris alpina) flocks (Davis 1980) could reduce the time predators have to align themselves with prey before an attack. Lastly, there is a suggestion that some predators may overestimate the speed of individual prey in a group (Milinski 1977b). Since some predators catch prey by interception, correct estimation of prey speed could be crucial for successful predation (Angel 1970, Curio 1976). It is difficult to envisage how these hypotheses could be tested for gulls preying on Puffins. For example, switching of attacks from one Puffin to another more often with large numbers of prey avail-

able could be interpreted as prudent use of time in a hunt if the probability of prey captive after prolonged pursuit was small. The same criticism applies to previous interpretations of some of the fish predation studies.

An instance of breakdown in school structure observed by Hobson (1968) when two schools travelling in different directions coalescedis particularly interesting in view of the tendency for hunting gulls to make attacks at wheel turn regions, since these are areas where there is often a two way traffic of birds flying in adjacent wheels.

With increasing numbers of Puffins in the air, gulls took longer to make a kill, dropped more catches (an indication of inefficiency in closing on the prey) and ranged farther while hunting. These findings are similar to data on the behaviour of fish predators, suggesting that large numbers of flying prey reduce the predatory efficiency of gulls through a confusion effect.

Optional Foraging and Models of Gull Behaviour

Models of gull hunting behaviour presented in this chapter were based on simple assumptions, such as that gulls might hunt during any one day only as often as was necessary to meet food requirements for that day. A model 'can be tested either by a direct test of its assumptions or by comparison of its predictions with observation' (Maynard Smith 1978). Comparison of model generated hunt frequencies with observed hunt frequencies indicated that gulls met feeding requirements by hunting less than would be expected from this simple model. Theories which suggest how animals might make decisions about when, where and how often

to forage may thus help interpretation of gull hunting behaviour.

Theoretical work on the efficiency of animal foraging behaviour originated with the papers of Emlen (1966) and MoArthur and Pianka (1966). Studies and models of foraging behaviour have burgeoned since this date (reviewed by Pyke et al 1977). Optimal foraging theory, as this body of work is known, is underwritten by an implicit or explicit acceptance of neo-Darwinian natural selection theory. Optimisation models do not demonstrate that organisms optimise their foraging behaviour. Rather, by assuming that an animal will, as a result of natural selection, tend to harvest food efficiently, they seek to identify the decision rules which may be used by the animal to maximise foraging efficiency, usually measured in terms of energy (e.g. Schoener 1971, Krebs 1978, Maynard-Smith 1978).

Models to date have been mainly concerned with four problems : choice by the animalof which types of food to eat (optimal diet); choice of which patch type to feed in (optimal patch choice); allocation of time to different patches; and optimal patterns and speeds of movement (Pyke et al 1977). The last three sets of models are relevant to the discussion of gull hunting behaviour and the first set to the theoretical relationship between Puffin numbers and gull predation.

A 'patch' is an area within the feeding habitat whose boundaries may be identified by changes in the forager's own behaviour (Hassell and Southwood 1978). For example, if a bird makes foraging movements in one area, flies over an

adjacent area without foraging, then lands and makes further foraging movements in another area, the first and last areas are 'patches'.

Gull behaviour suggests that Puffin wheel turn points can be considered foraging 'patches'. Gull foraging patches, so defined, are fixed in space, but of variable quality, in terms of prey abundance, in time. Pyke et al (1977) consider that if an animal can learn the location and types of patches in an area, it can 'accept' or 'reject' patches before attempting to feed in them, and specialise in foraging in certain patches. This is analogous to the behaviour of predatory gulls, where birds standing at vantage points can monitor prey abundance in core hunting areas before beginning to hunt.

A pair of gulls require to kill sufficient Puffins to meet the energy requirements of the two parents and their chicks during the breeding season. Killing Puffins in excess of these requirements would not increase the fitness of a breeding gull, and might reduce fitness by diverting time from other activities such as preening or watching for predators. Schoener (1971) has theorised that given these assumptions, an animal's fitness should be greatest when it minimises the time required to obtain the fixed amount of energy and uses the time left over to perform the other activities, such an animal being referred to as a 'time minimiser'. Using the length of the nestling period as a time scale, as in the models presented above, these assumptions give a good description of gull hunting behaviour. Gulls hunt most often when hunting is likely to lead to a

quick kill. There is a discrepancy between kills and a pair's energy requirements if considered on a time scale of single days, but not if kills are considered across a larger time scale.

The movement patterns of foraging animals have mainly been studied in insects. Predators, birds and insects often alter their movement path after finding prey by increasing their rate of turning and/or decreasing speed of movement in 'area restricted searching' (Tinbergen et al 1967, Hassell and May 1974). This could increase foraging efficiency if prey are spatially clumped, the 'prudent' forager being an animal which spends most time where food is plentiful or most profitable (Royama 1970, Hassell and Southwood 1978). Reviewing foraging movement studies Krebs (1978) considered that 'random search is in fact highly inefficient - at least when the prey do not renew themselves extremely rapidly'. In a review of insect predator and parasite movements Pyke (1978) felt that movements described by some authors as 'random' were better described as 'independent of external stimuli' and by his criterion 'certainly not random'.

If prey can build up again in a patch after depletion, a forager which exhibited area restricted searching could time successive visits to the patch on the basis of prey renewal rate, the predator being able to determine optimal return time through its own foraging efficiency (Charnov et al 1976). The presence of intruders which depleted the patch in the animal's absence could interfere with evaluation of efficient return times. In such circumstances, defence of a feeding area, based on characteristics of prey renewal,

would be a good strategy. This idea has been used to explain defence of feeding territories in Sunbirds (Nectarinia reichenowi) by Gill and Wolf (1975). It is also applicable to the behaviour of hunting gulls. Gulls restrict their hunting searches mainly to Puffin wheel turn areas, but also visit other areas. Few attacks on Puffins are made at these other areas.

Consideration of optimal return time theories suggests that gull movements away from wheel turn regions might be influenced by the behaviour of Puffins in the favoured hunting area. Since gulls usually return in less than three minutes to core areas, prey renewal in the wheel may be rapid. Defence of hunting space while hunting, as observed in Dun gulls, would thus seem a good strategy, but defence of a hunting area at other times, not usually observed in neighbouring pairs sharing core areas, would be unnecessary and potentially costly.

Consideration of gull hunting behaviour through models and in the context of optimal foraging theory suggests some of the decision rules which gulls may use for efficient foraging. Discussion of gull behaviour in this framework suggests avenues for future research. For example, it would be useful to know how the number of Puffins in a wheel changes during short periods of a hunt when a gull is flying in, or outwith wheel turn regions.

Puffin Numbers and Gull Predation

The sub-population of Puffins in the Sparse area of Dun cannot survive under present levels of predation without much immigration (Harris 1980). There are a few examples

from other species of predation exterminating or severely reducing local prey populations. For example, weasels (Mustela erminea) exterminated a lemming (Lemmus lemmus) population in northern Canada (Maher 1967), and Barasingha deer (Cervus duvauceli) declined as a result of predation by tigers (Panthera tigris) on a small localised population whose annual recruitment was poor (Schaller 1967). There is much conflicting evidence on the relationship between numbers of predators and prey, particularly in the literature on predator-prey 'cycles' (e.g. see review in Emlen 1973).

Optimal diet theory - which addresses the problem of how a predator could maximise its net rate of energy intake while foraging - has a bearing on the question of whether gulls breeding in the Sparse area will continue to exploit Puffins at the present level. It is also relevant to possible gull-Puffin interactions at other localities.

Some models of optimal diet predict that if the encounter rate with profitable prey is low, the predator should be unselective, but if profitable prey are abundant, the predator should ignore lower quality prey, independent of the density of low ranking prey. (Prey items in the diet are ranked according to E/h values, where E is the energy content and h the handling time of the prey (Macarthur 1972, Charnov 1976)). Laboratory studies of Great Tits (Parus major), and a field study of Redshank (Tringa totanus) have given quantitative support to the idea that as the density of profitable prey increases, predators become more selective (Krebs et al. 1977, Goss-Custard 1977). Data on the diet of gulls

on Dun and Hirta presented in the previous chapter lends qualitative support to the relevance of these models to gull diet. Gulls in the Ruival area on Hirta have access to a much lower density of Puffins than birds on Dun. Midden contents indicated that Ruival gulls ate a wider variety of prey than Dun gulls. Also, gulls in the Sparse area included more adult avian prey of species other than Puffins in their diet than gulls in the Dense area.

Optimal diet theory suggests that as Puffin density in the Sparse area declines, gulls breeding there should become less selective in their predation. This implies that a Sparse Puffin's risk of being killed by a gull will not necessarily increase as Puffin density in that area decreases. Access to patches of high density Puffins in the Dense area would complicate this simple picture, but on the basis of observations on hunting area defence it can be assumed that Sparse area gulls have only limited access to the high density sites.

For other localities, optimal diet theory gives a means of explaining observed prey choice by gulls, and possible prey choice at sites not yet studied. Namely, if prey with a higher E/h value than Puffins are sufficiently abundant, Puffins may be ignored altogether, or included only as a function of fluctuations in higher ranking prey. A Puffin's risk of predation at any site is thus both a complex function of Puffin density, and related to the abundance of other prey species. Comparative data on gull diet in Britain, Iceland and Russia presented in the previous chapter, which indicates how gulls at different localities tend to specialise on

different prey types, even when Puffins are available, also lends qualitative support to these ideas. Modelling gull prey choice on the basis of prey densities at different sites should be feasible using an optimal diet framework.

GULLS AND PUFFINS ON DUN - Conclusion to Chapters 1 and 2

Several studies on Dun have indicated that gull predation on Puffins is influenced by variations in Puffin numbers within and between different sites on the island. Core hunt areas used by gulls are associated with Puffin wheels, but it appears that not all regions where Puffins wheel are equally suitable for sustaining predatory gulls throughout the breeding season. The suggestion of more than 64 possible core hunt areas on the island made earlier on the basis of known wheels and the extent of core area overlap is thus an overestimate. The maximum number of gull pairs attempting to breed during the study period was 40 in 1977, where breeding failures early in the season were associated with few Puffin corpses being found near the nests. The available evidence suggests that the number of gull pairs breeding on Dun was close to, or even in excess of, the number which could successfully raise young on a diet of Puffins. Assuming that conditions remain unchanged it is predicted that the annual rate of predation on Puffins will not increase.

Small fluctuations in Puffin density in the Dense area - either increases or decreases of the order of several thousand pairs, as have been observed in recent years (Harris and Murray 1977, Harris 1981), should not alter the number of gull pairs able to exploit this area. Further decreases in Puffin density in the Sparse area, as have also been observed in recent years, should initially have no influence on the gulls exploiting this area, but eventually reduce the number of gull pairs regularly hunting there.

Predation of Sparse area Puffins by Sparse area gulls may thus eventually decrease before extinction of this local Puffin colony area. However, Sparse area Puffins would still under these circumstances be open to occasional attack from gulls which normally hunted in the Dense area. Also, when nesting density becomes very low, young Puffins reared in the Sparse area and prospecting for nest-burrows may be attracted to the flourishing Dense area, where there still appears to be room for more pairs, rather than to their natal area, where they see few other Puffins. Thus, gull predation might nevertheless force the Sparse Puffin area to extinction.

Evidence from previous studies indicates that the Puffin breeding population in the Dense area could maintain itself under current levels of predation (Harris 1980). While predation by gulls could cause a continued decline in Puffins breeding in the Sparse area, there is no reason to suppose from the present study and previous work on Dun that future predation will adversely affect stocks of Puffins in the Dense area.

Considering the influence of gull predation on Puffins more broadly: Predation could be a selective force leading Puffins to breed in large, high burrow density colonies. It could also lead Puffins within such colonies to synchronise their colony attendance and flights at the colony with large numbers of other Puffins.

Large, high density colonies are the typical breeding site for the majority of Puffins outside the high Arctic. The next chapter investigates whether individual Puffins at such colonies synchronise their movements with large numbers of other Puffins.

CHAPTER THREE

Synchronisation of movements to, from and within the breeding colony by groups of Puffins

Plates 3.1 and 3.2 Outer and inner tracks of a wheel over Dense Area B

" Tell me Genry, what is known? What is sure, predictable, inevitable - the one certain thing you know concerning your future and mine? "
" That we shall die. "
" Yes. There's really only one question that can be answered Genry, and we already know the answer....the only thing that makes life possible is permanent, intolerable uncertainty : not knowing what comes next."

Ursula K. le Guin 'The Left Hand of Darkness' Panther 1973.

INTRODUCTION

Data presented in Chapter Two indicates that individual Puffins could reduce their risk of predation by gulls through synchronising their movements with large numbers of other Puffins. Most gull attacks were made on wheeling birds, the success of these attacks declining with increasing numbers of Puffins. Consequently did the structure of wheels change with increasing numbers of Puffins and/or a hunting gull in the vicinity?

Wheeling - (flight in an elliptical track over a colony area, out over an adjacent sea area and in again to the colony track - see Appendix 1) - has already been described qualitatively (cf. Lockley 1953, Myrberget 1962, Skokova 1962, Nørrevang 1977). The present study quantifies aspects of the structure and temporal duration of wheels, and the behaviour of individual Puffins in wheels. Information on wheels is used to assess the influence of predatory gulls on flying Puffins. Wheel data is presented in the context of information on other aspects of Puffin colony attendance to investigate the question - Do individual Puffins synchronise their movements to, from and within the colony with large numbers of other Puffins?

STUDY SITES

Comparative data on wheeling in the presence and absence of predatory gulls was collected on Dun, St Kilda. Patterns of attendance in different colony areas were documented on Dun and on the Isle of May. Movements of birds to and from fishing grounds were observed mainly on St Kilda and at Vik,

Iceland. Qualitative observations were also made on Mykines, Faroe Islands and Grimsey, Iceland.

METHODS

Numbers of birds in water flocks were counted through binoculars and the timing of movements to and from flocks recorded on cassette tape. Behaviour of water flock birds was scored using focal animal sampling (Altmann 1974), each bird being watched for one minute. Definitions of different behaviour classifications used are given in Appendix 1. Day to day variations in numbers of Puffins in wheels were recorded using the 'low' to 'very high' classifications quantified in Chapter 2. Sketches of wheels were made on 1 : 7600 and 1 : 6034 scale maps for the Isle of May and Dun respectively. The behaviour of individual Puffins in wheels was observed from concealed vantage points on Dun. Focal animal sampling was used in these observations, each Puffin being watched for at least one wheel circuit unless it left the wheel before completing a circuit. Wind speed readings were taken with a hand held 'Ventimeter' anemometer. Burrow density data for Dun Puffins is taken from Harris and Murray (1977). Methods used in studies of Puffins flying to and from fishing grounds, and in photographic studies are described later.

RESULTS

3.1 DIURNAL PHASING OF LARGE SCALE MOVEMENTS TO AND FROM THE COLONY

In the pre-laying period, water flocks usually formed

off the Isle of May from mid-morning. Birds were initially distributed in small groups of less than ten 100 metres or more offshore. In the initial phase of water flock build up there were no birds ashore at the colony, new landers in water flocks arriving from farther out to see. Each water group was transient, Puffins from one group frequently joining, or being joined by, members of other groups (Fig. 3.1). Single Puffins landing in a water flock tended to swim close to other Puffins within a minute of landing.

The behaviour of Puffins in 'groups' of less than or equal to two and greater than two birds was different. Pairs split up significantly less than larger groups (Fisher exact $p = 0.024$, $N = 58$) (Table 3.1). Single Puffins and pairs spent more time actively swimming than larger groups and singletons preened more than other birds (Fig. 3.2). Singles and pairs also head-shook more, this behaviour not being associated with preening in the way it was for larger groups (Tables 3.2, 3.3, 3.4). Birds in pairs head-shook and head flicked more than other birds (Fig. 3.3). (Head flicking is a male pre-copulatory display.) Rise-up wing flapping was associated with preening in groups of all sizes in the early stages of flock build up (Table 3.5). Birds in groups of three or more spent most of their time sleeping or floating. Thus, after landing in the water, an individual Puffin initially preened and swam around, but usually joined other Puffins within a minute, spending much of its time sleeping after this. Pairs of Puffins were frequently involved in courtship activities and tended to stay together in the water.

Water-flock behaviour - non overflight periods

Table 3.1

	Pair	> Pair	Group splitting
Split up	1	18	19
No split	12	27	39
	13	45	58

$p < 0.05$ Pairs split up less than larger groups (Fisher exact test).

Table 3.2

	≤ Pair	> Pair	Head-shake
+ Head-shake	15	23	38
- Head-shake	42	154	196
	57	177	234

$p < 0.05$ Pairs, singles head-shake more than other group birds ($\chi^2 = 4.69$).

Table 3.3

≤ 2 birds

	+ Preen/Wash	- Preen/Wash		Head-shake/ Preen
+ Head-shake	5	11	16	a)
- Head-shake	11	30	41	
	16	41	57	

$p \geq 0.1$ Head-shake no association with preening for groups ≤2 ($\chi^2 = 0.00003$).

Table 3.4

≥ 3 birds

	+ Preen/wash	- Preen/Wash		Head-shake/ Preen
+ Head-shake	12	11	23	b)
- Head-shake	13	141	154	
	25	152	177	

$p < 0.01$ Head-shake association with preening for groups ≥3 birds ($\chi^2 = 28.05$).

Table 3.5

	+ Preen	- Preen		Rise-up Wing Flap/Preen
+ RUWF	13	10	23	
- RUWF	28	183	211	
	41	193	234	

$p < 0.01$ Rise-up Wing flap association with preening ($\chi^2 = 23.94$).

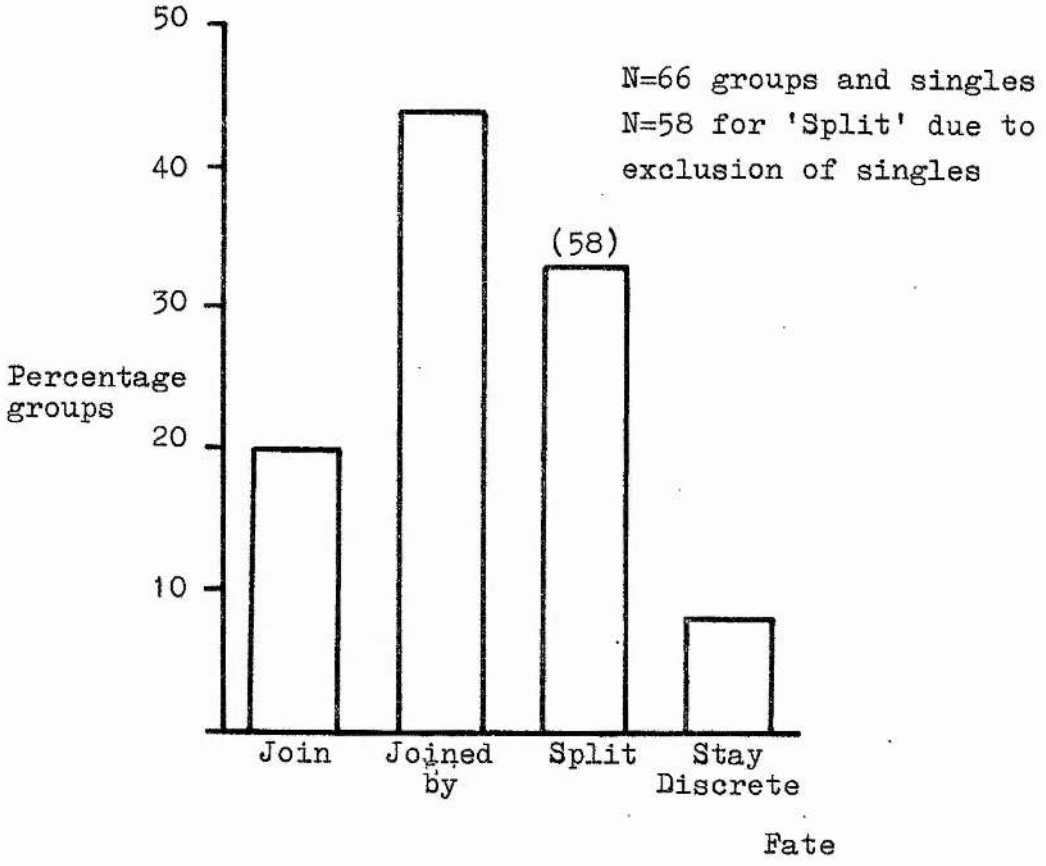


Fig. 3.1 Fate of water groups per minute. Isle of May April 1977

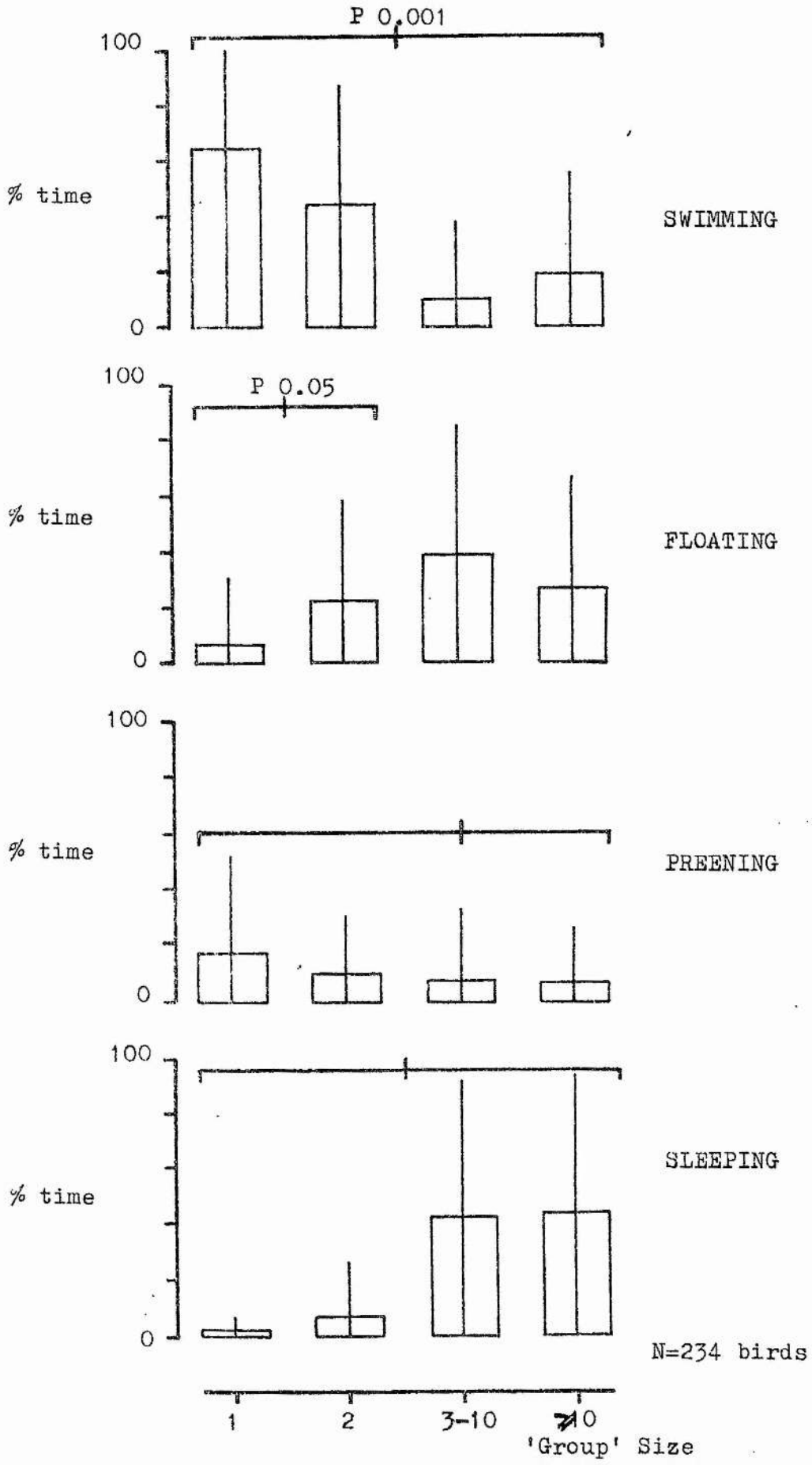


Fig. 3.2 Time spent performing different behaviours by Puffins in water flocks

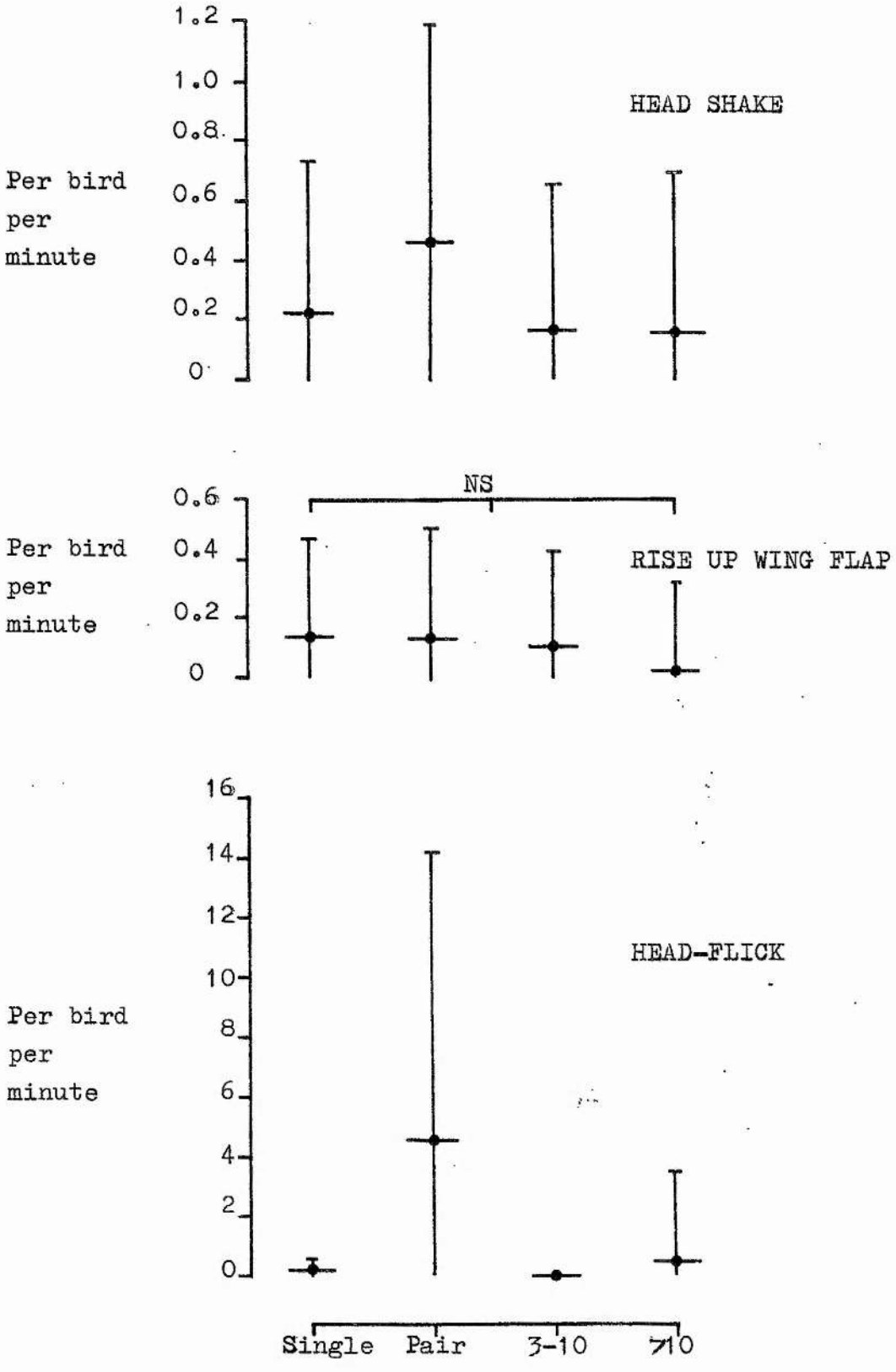


Fig. 3.3 Frequency of short duration behaviours among Puffins in water groups

As water numbers built up, there could be a rapid change in the distribution of birds, with small groups coalescing to form flocks of thirty or more, or even all birds coalescing in one large flock. Flock members were at this stage alert (Table 3.6) and made 'milling' to and fro swimming movements. At this point, many birds might take off and begin flying over the flock area in erratic low passes before landing again. Flock birds Rise-up wing flapped more frequently at this stage (Table 3.7). Overflight of water flocks could be brief, but if many Puffins joined the flight, the flight pattern usually changed. In this new pattern flying birds tracked in to the land and flew over a colony area adjacent to the water flock before turning out to sea again. This was the onset of wheeling. The pattern of water flock build up, overflying and wheeling at the Burrian area on two April days in 1977 and 1978 illustrates the temporal association between water group merger, overflying and wheeling (Figs. 3.4; 3.5).

If wheeling continued, water flock birds swam close inshore. Landings at the colony might occur at this time, landers initially grouping on rocks or grassy hummocks. Landings were clumped temporally as well as spatially. Deviation of observed landing times from random in three colony area occupation periods on Rona is shown in Table 3.8. In each case, deviation from random, as judged by Chi-squared values, was mainly due to there being too many time intervals with no landings and with more than two landings (Fig. 3.6).

Water-flock behaviour - overflight versus non overflight periods 11/4/78 18.00 18.30 GMT

Table 3.6

Sleep	+ overflight	- overflight	
+ Sleep	-	21	21
- Sleep	10	9	30
	10	30	40

$p < 0.0001$ Birds less likely to sleep during overflight periods. (Fisher exact test).

Table 3.7

RUWF	+ overflight	- overflight	
+ Rise-up Wing Flap	6	2	8
- RUWF	4	16	20
	10	18	28

$p < 0.05$ Rise-up Wing Flap more likely in overflight period. (Fisher exact, $p = 0.0111$).

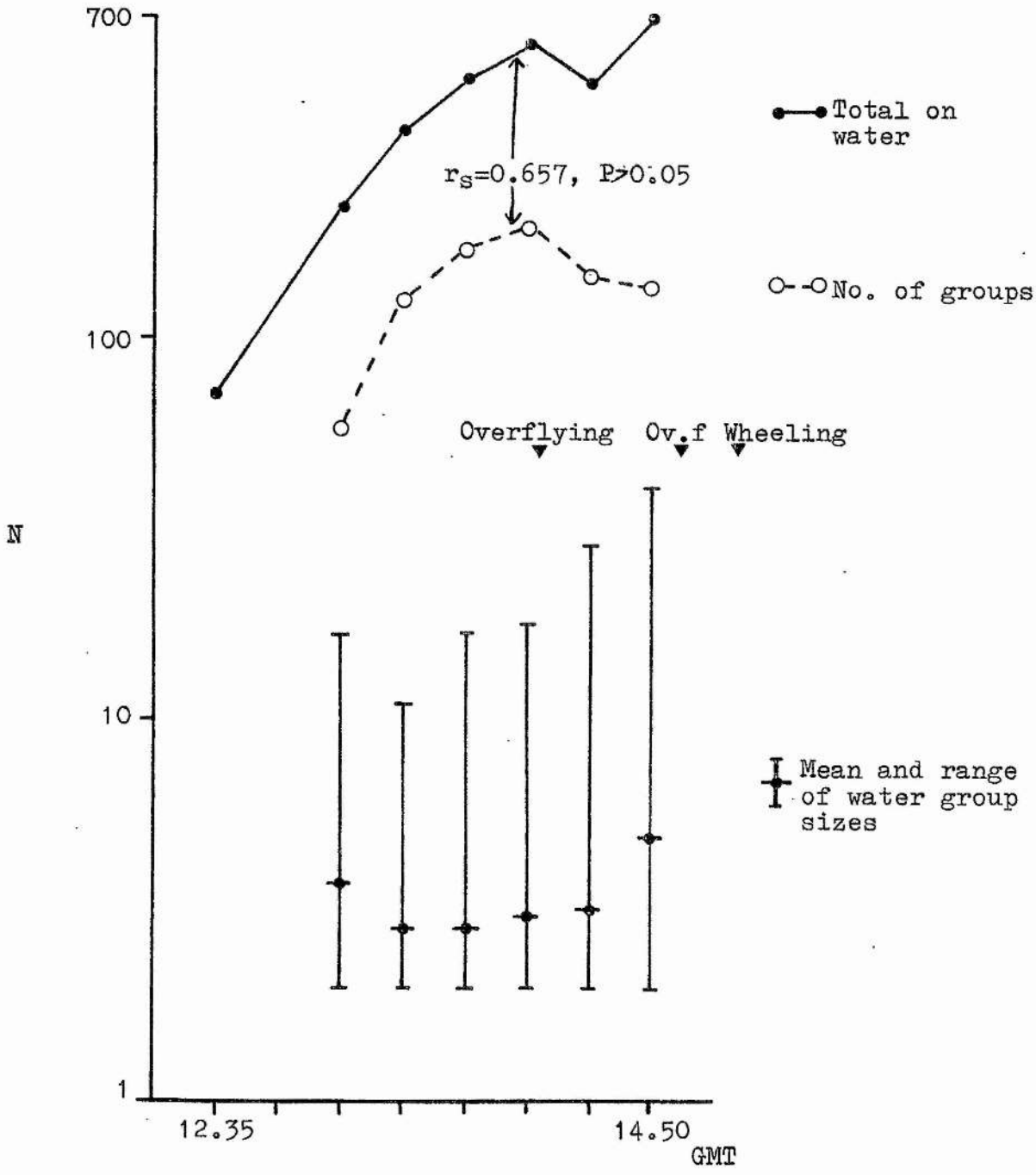


Fig. 3.4 Build up of water flocks off Burrian, 12/4/77

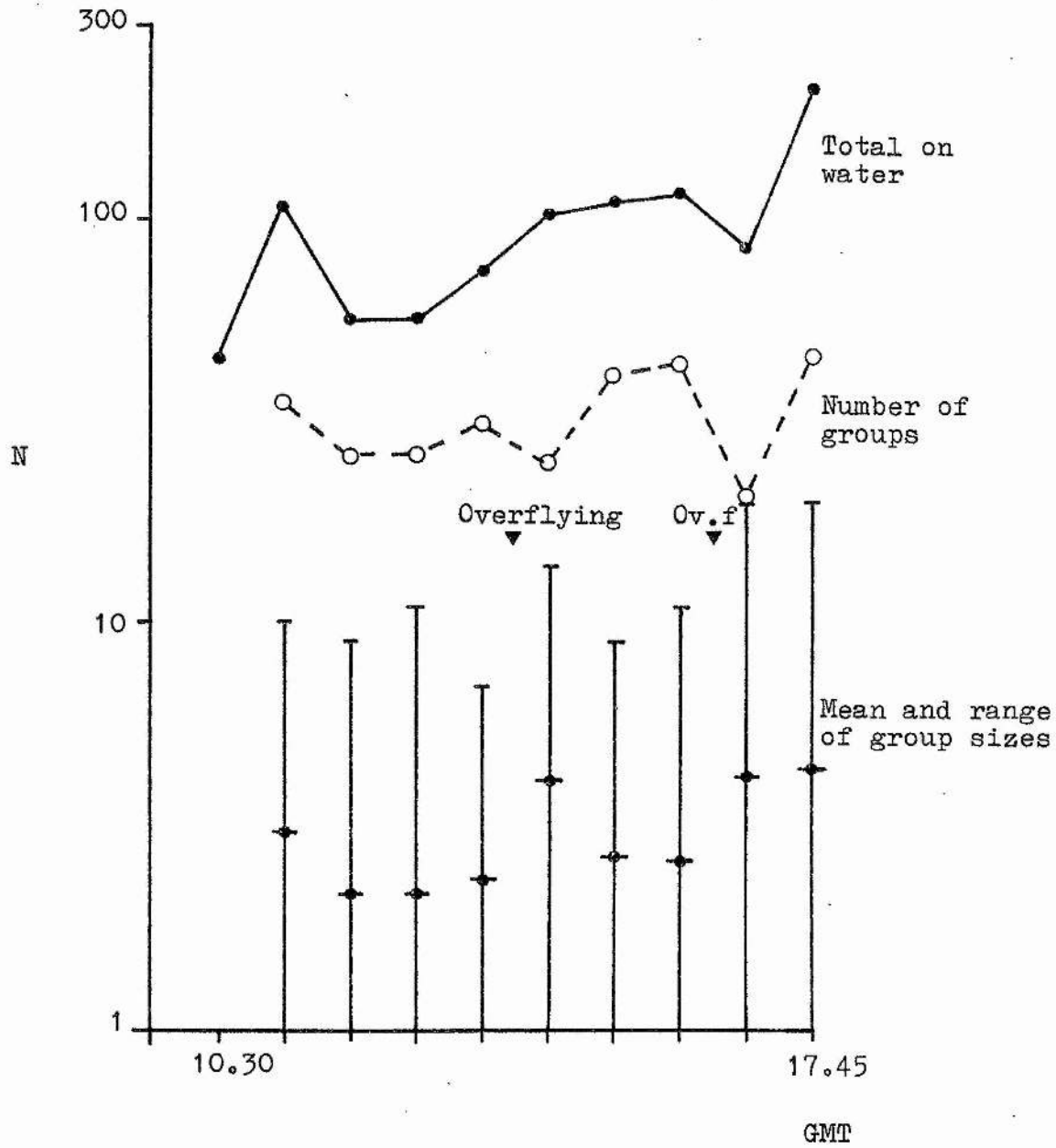


Fig. 3.5 Fluctuations in water flocks off Burrian, 25/4/78

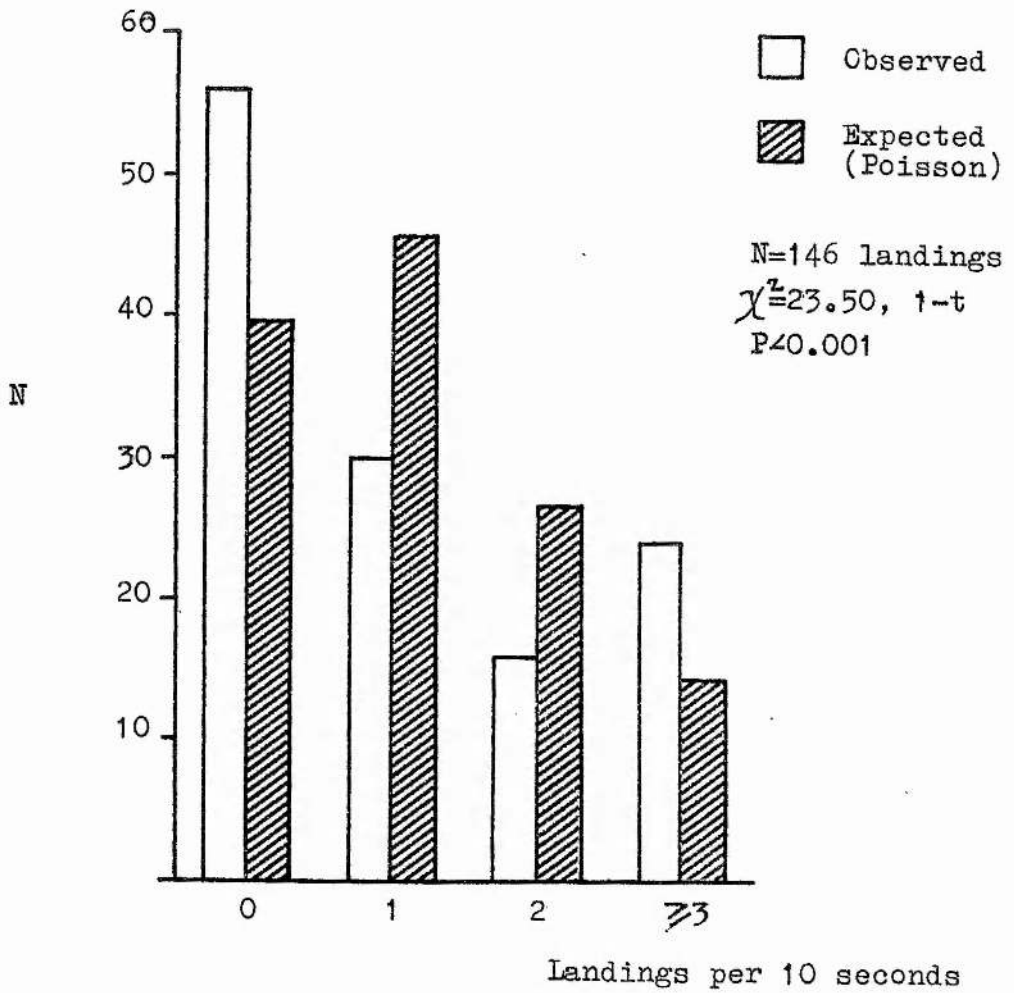


Fig. 3.6 Puffin landings from wheel during early part of Rona occupation period, Isle of May 19/4/78

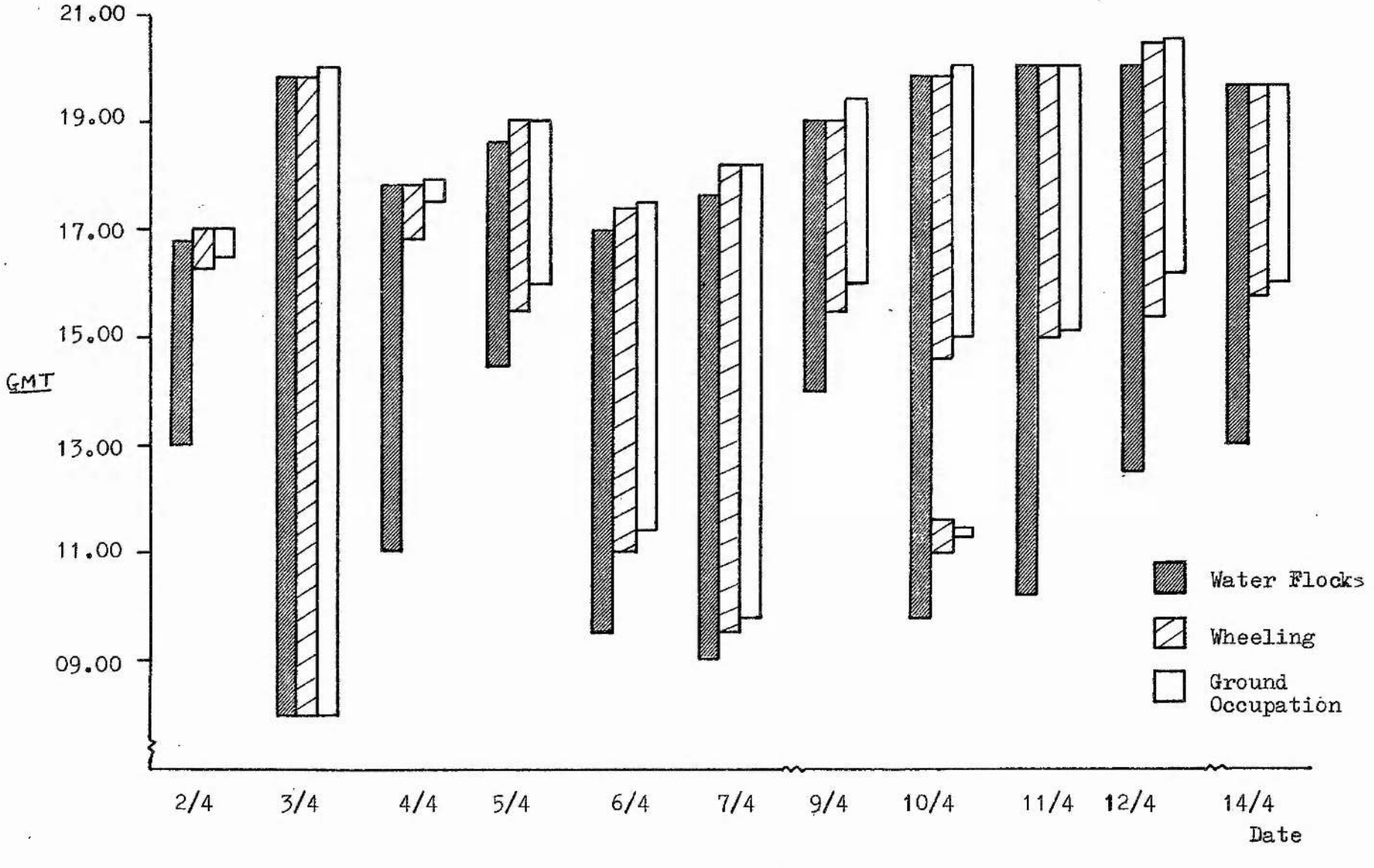
Table 3.8 Puffin landings from wheel during early part of Rona area occupation periods, Isle of May.

Date	Observation period (mns)	Time window (secs.)	Landings	$\bar{x}$ Landings per window	χ^2	df	p - random
17.4.78	40	10	201	0.8625	6.29	2	0.05
19.4.78	21	10	146	1.159	23.50	2	0.001
22.4.78	24	10	189	1.3125	14.69	2	0.001

Data for the Burrian area for early April 1977 illustrates the sequencing of water flocking, wheeling and ground occupation (Fig. 3.7). If ground occupation continued, birds began to move from grouping areas to burrows. Water birds remained inshore, numbers staying fairly stable until dusk. On the Isle of May, the number of birds wheeling over the occupied area declined. Wheel numbers might increase again around dusk. (This feature of Puffin social behaviour is well documented, cf Lockley 1953). At dusk, water flock numbers diminished as birds dispersed to roost farther out to sea. Data on water flocks off Dense and Sparse areas of the Dun Puffin colony illustrates this dusk decline in water numbers, although the data does not show the eventual disappearance of water birds, since darkness made accurate counting impossible (Figs. 3.8, 3.9). The usual diurnal pattern of colony attendance, from water flock formation to colony desertion, is summarised schematically in Fig. 3.10.

The phasing of group behaviour was often different for different parts of the Isle of May colony. For example, one part of the colony could have birds ashore before flocks even began to form in the sea off another part, as is illustrated by data

Fig. 3.7 Diurnal phasing of water, air and ground grouping activity, Burrian April 1977



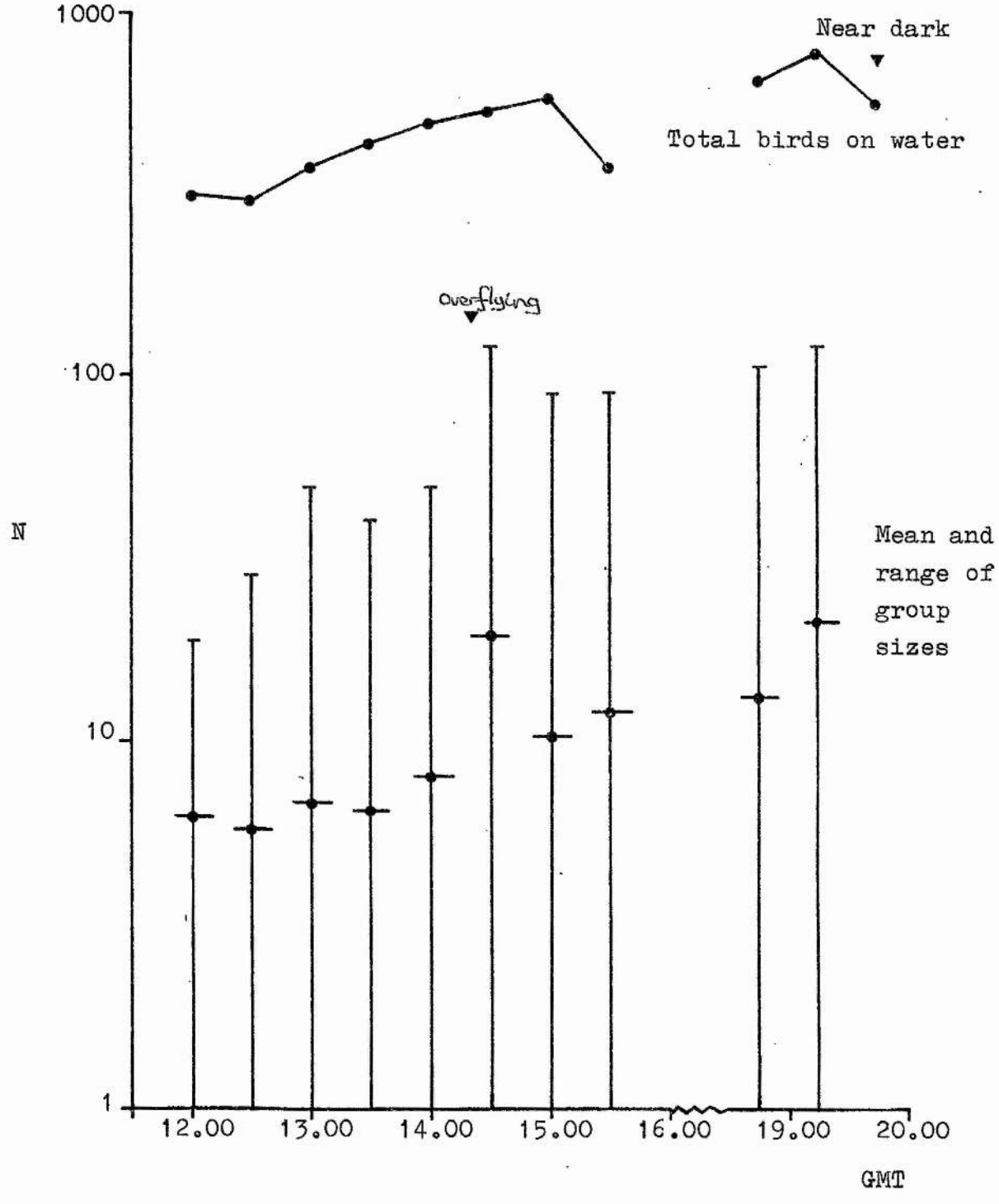


Fig. 3.8 Fluctuations in water flocks off Dense Area, 8/5/77

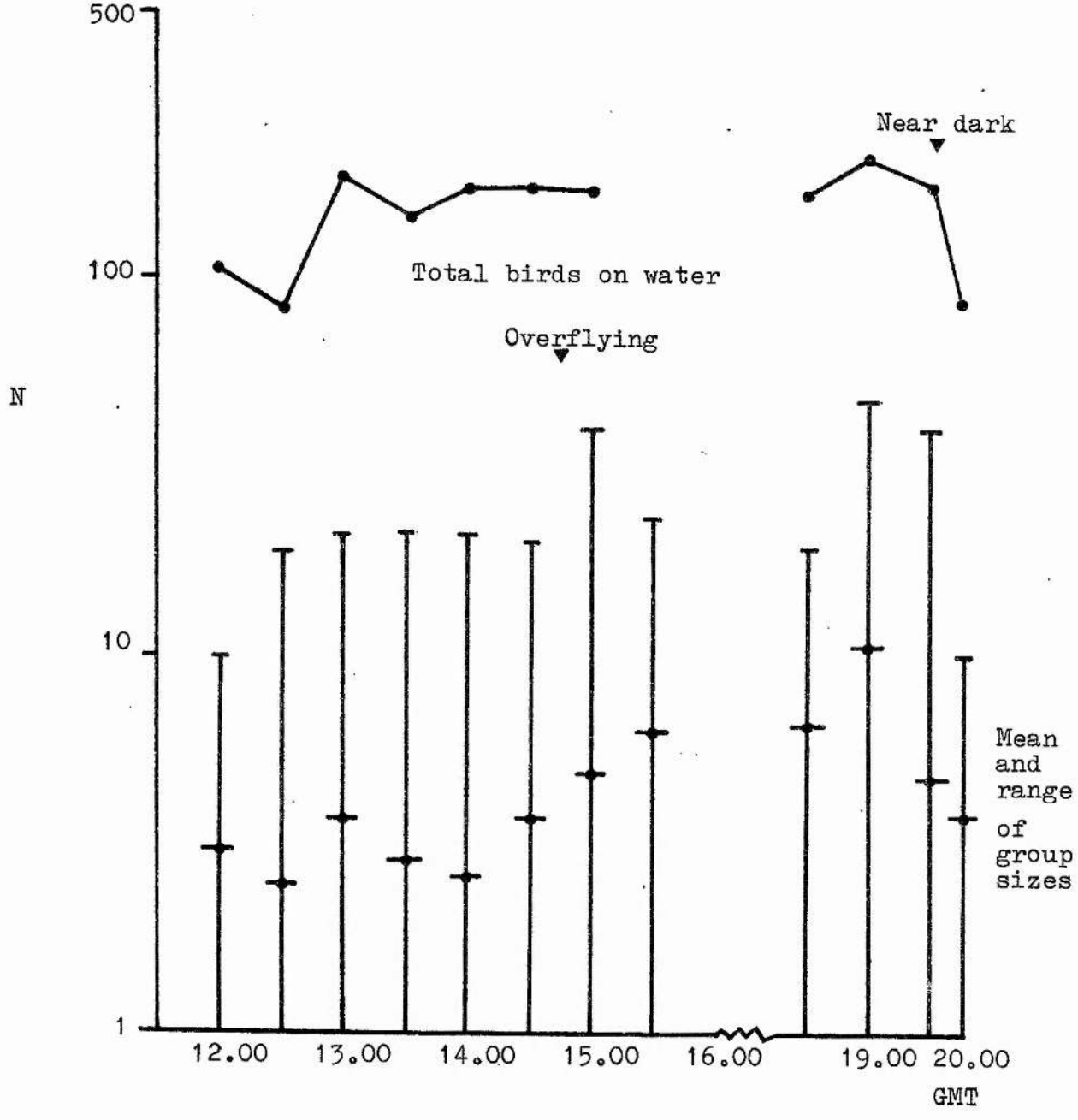
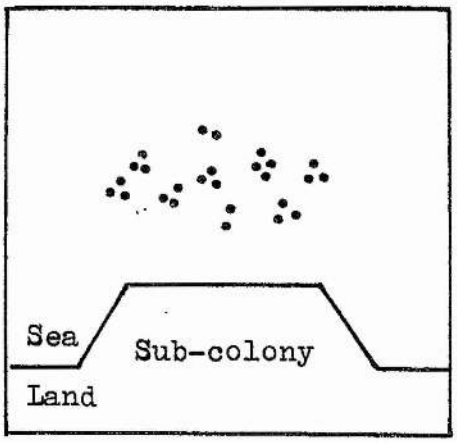
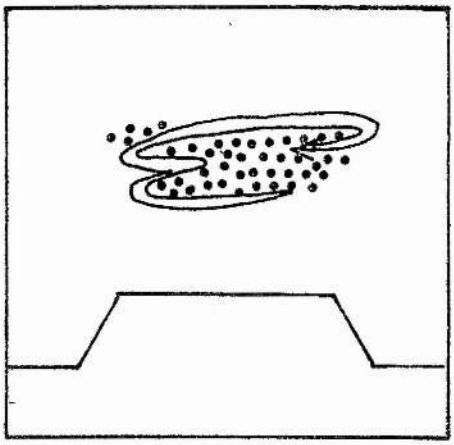


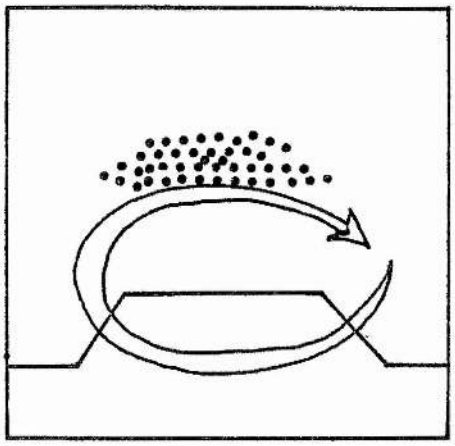
Fig. 3.9 Fluctuations in water flocks off Sparse Area, 8/5/77



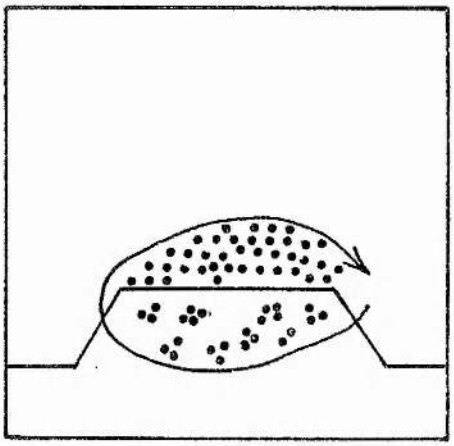
a. Water flocks form



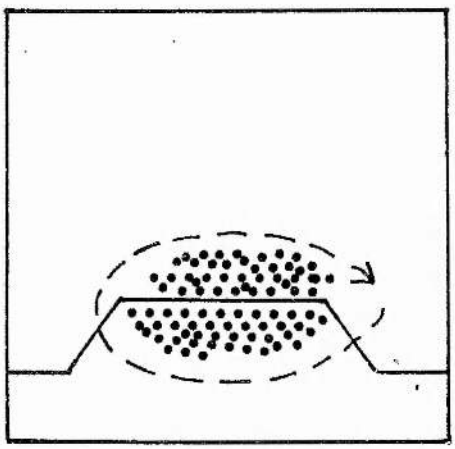
b. Flocks net, sea overflying starts



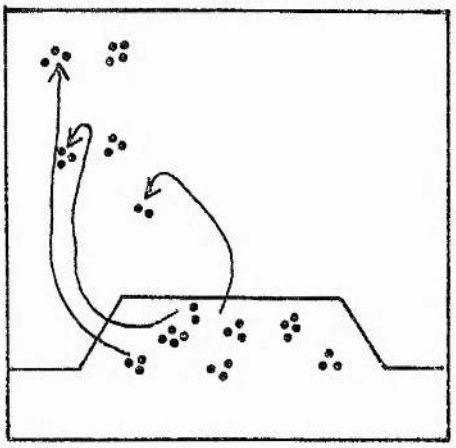
c. Wheeling over ground area



d. Flocks inshore, landers bunch ashore, wheel strength lessens



e. Burrows occupied, wheel strength slight



f. Sea flocks scatter, birds ashore bunch, wheeling only by a few birds

Fig. 3.10 Schematic phases of Puffin sub-colony occupation

for 12 April 1977, when birds were ashore at Little Hole before flocks had begun to form south of Colm's Hole (Fig. 3.11). On this day there was no landfall at all at the South Island area, although birds were present offshore and there was brief wheeling. Wheels over adjacent colony areas thus often started at different times. This is further illustrated by data for 12 May 1978 (Fig. 3.12). On this day an initial wheel over the main part of the Burrian colony quickly changed, as numbers increased, to two wheels over Colm's Hole and Little Hole areas. Wheeling west of Holyman's Road and at the Island area, about 30 metres west and 50 metres south of the Burrian areas respectively, did not begin until over an hour later.

In the pre-laying period in 1977, areas from the Burrian west and north to Rona tended to be first occupied in early afternoon. Areas near the south end of the island tended to be occupied in late afternoon or early evening, significantly later than the northern area (t - test $P < 0.05$) (Fig. 3.13). Although there was no difference in the overall timing of first landings at the more northern areas, this does not mean that within any one day the birds at different parts of this area landed at exactly the same time. For example, on 7 April 1977 there were a few birds ashore on the Burrian in the afternoon, but none elsewhere. This was particularly noticeable in 1978, when there was no landfall on the Burrian between 23 and 28 March, whereas birds were ashore at Rona and Horse Hole every day.

The number of birds ashore at the Burrian varied from day to day in the 1978 pre-hatching period (Fig. 3.14).

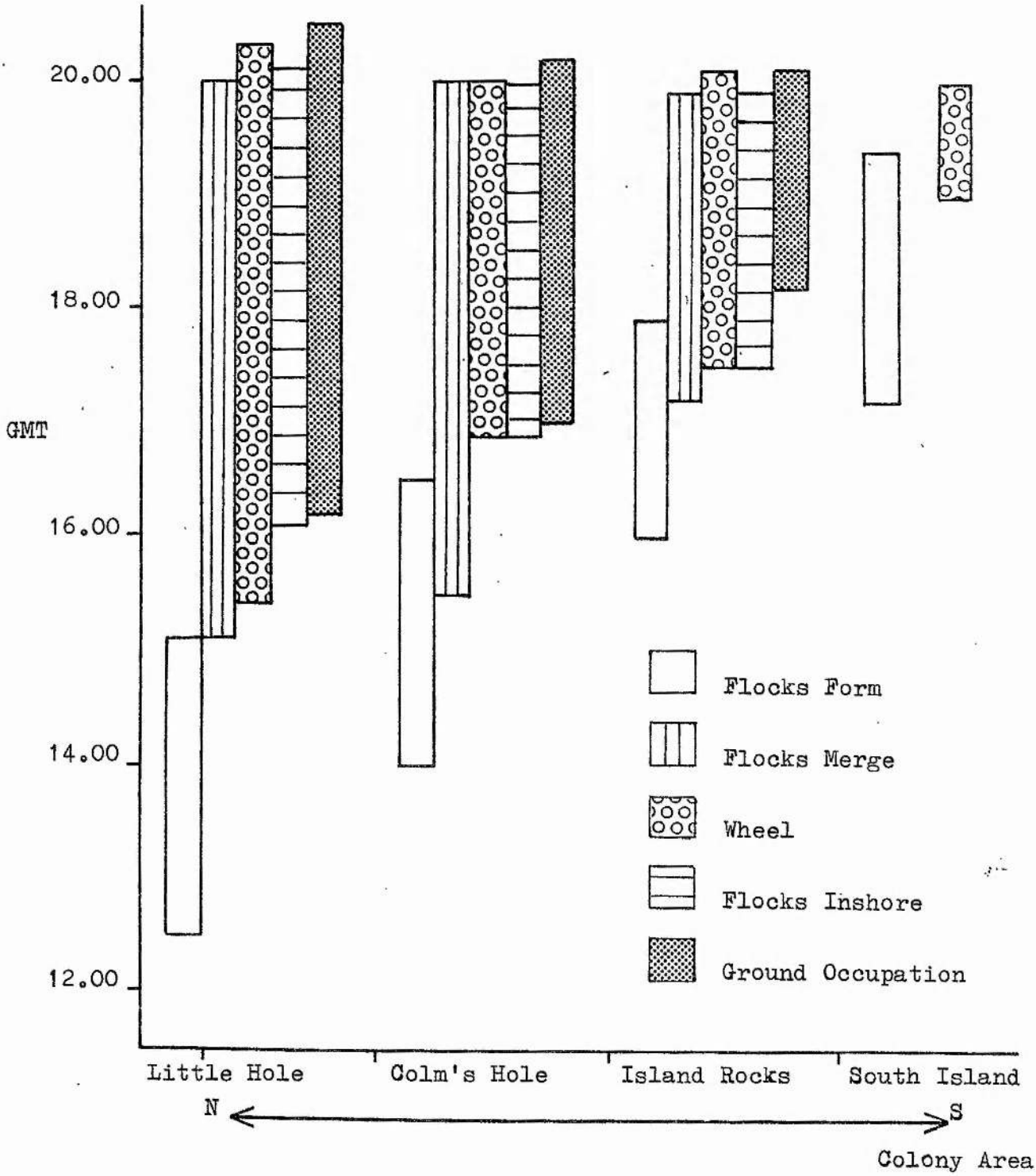


Fig. 3.11 Phasing of water, air and ground activity, Isle of May 12/4/77

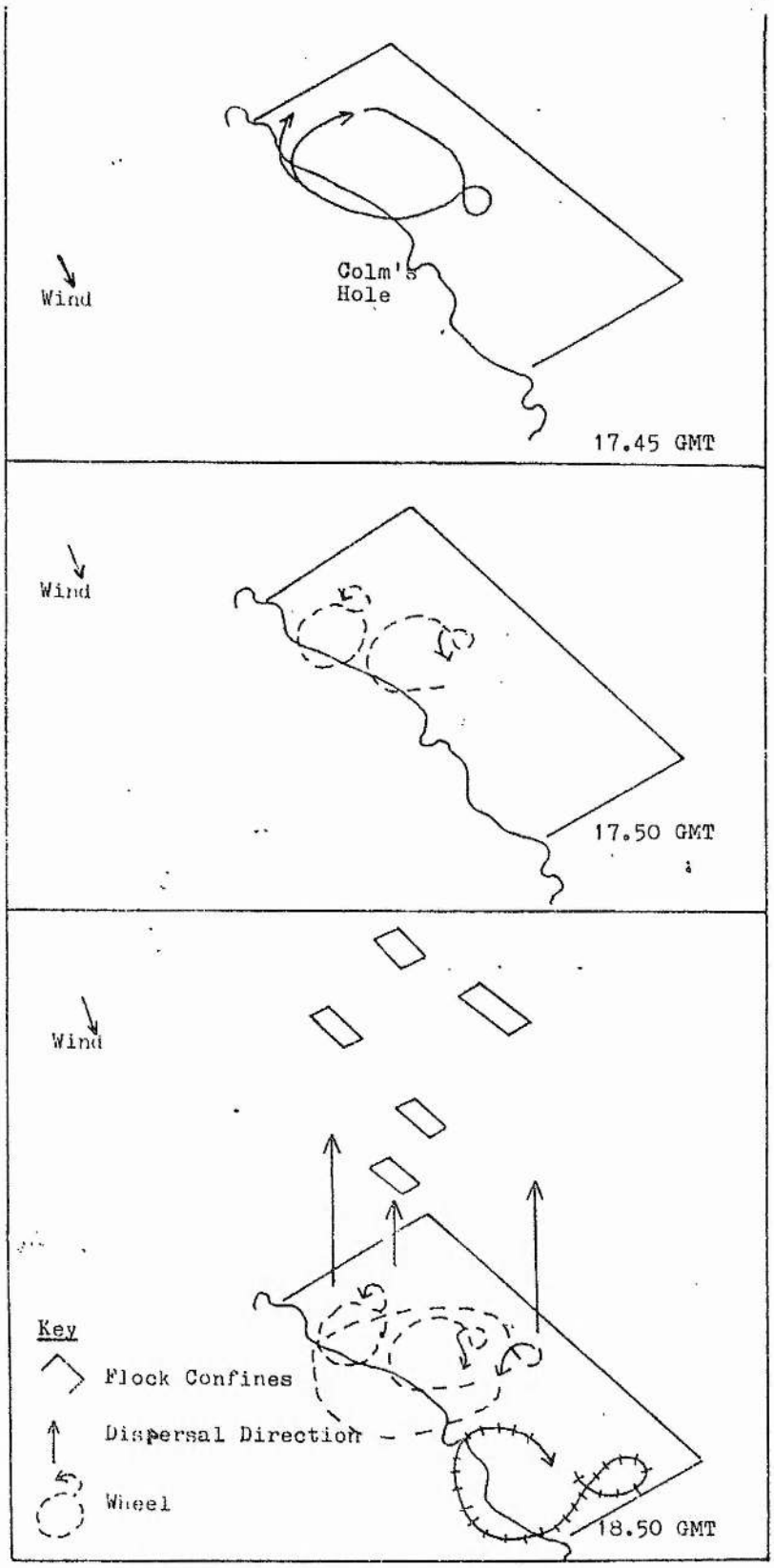


Fig. 3.12 Water flocks and wheels off Burrian, 12/5/78

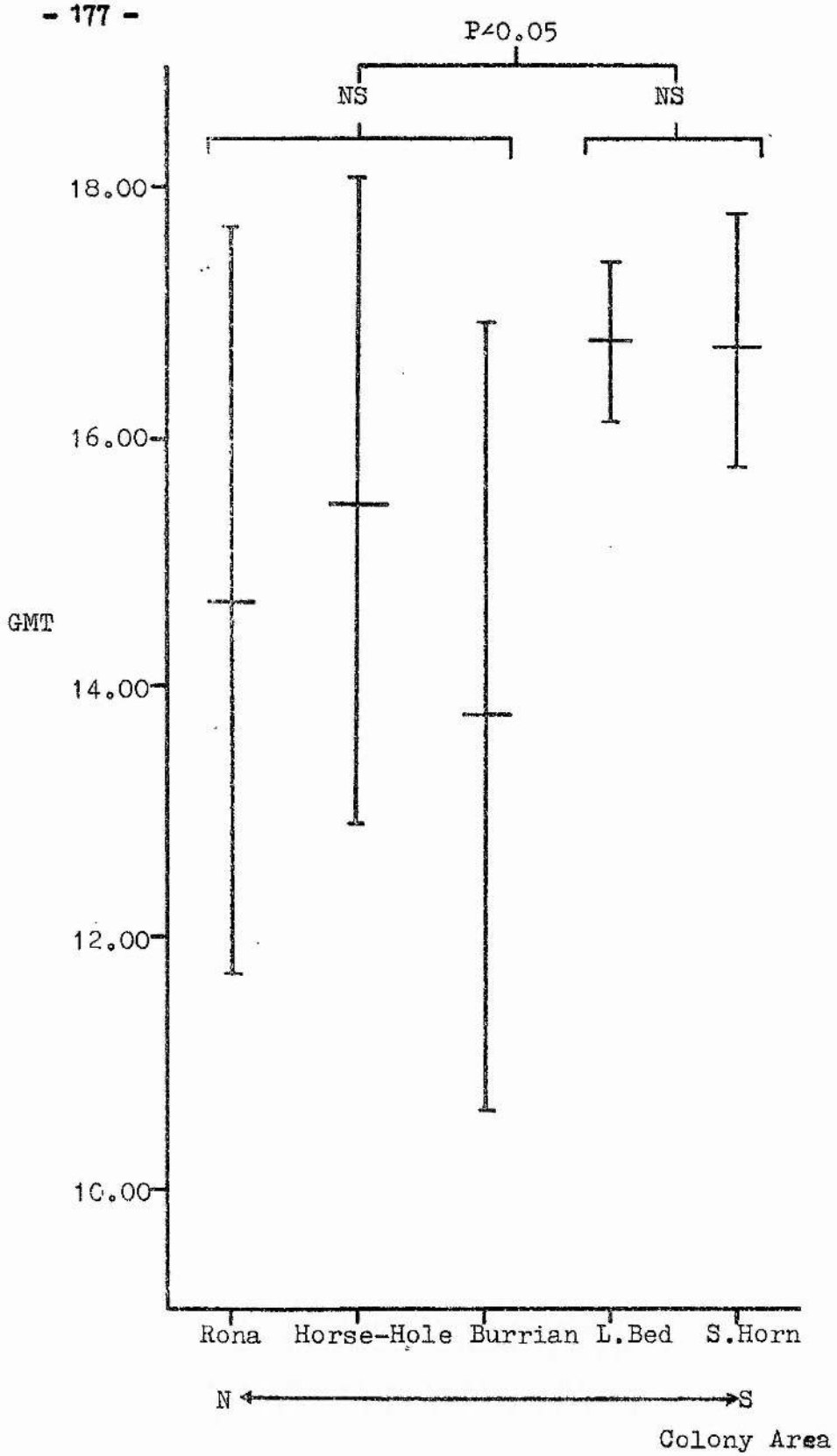


Fig. 3.13 Diurnal phasing of sub-colony occupation, Isle of May 2/4 to 14/4/77

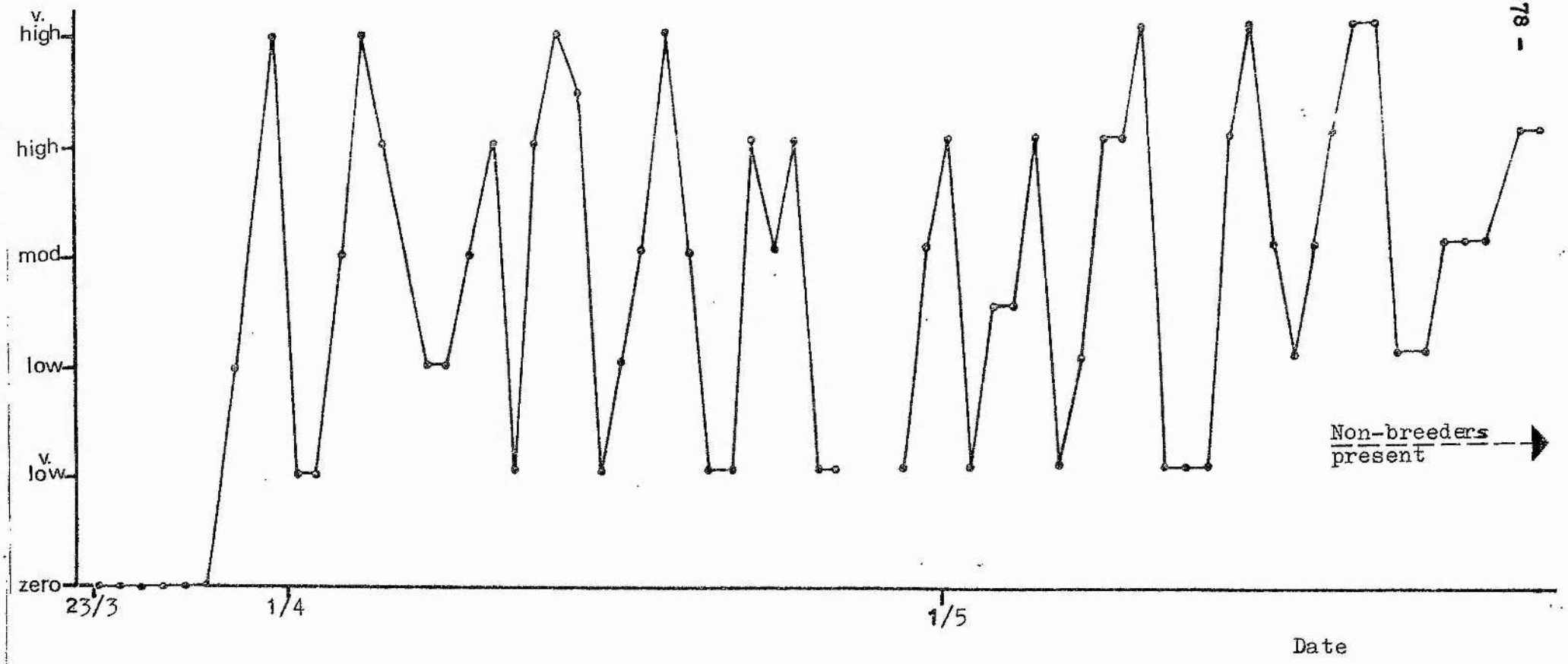


Fig. 3.14 Level of ground occupation at Burrian, Isle of May, 23rd March to late May 1978

Days where attendance was classed as 'very high' were always preceded by one to two days build up from 'very low' numbers. Peaks in Isle of May colony attendance occurred on average every four to five days in both pre-laying and incubation periods (Pre-laying $\bar{x}$ = 4.0 ± 0.58 days, 6 peaks, 25 days observation. Incubation $\bar{x}$ = 4.5 ± 0.76 days, 6 peaks, 30 days observation; $t = -1.32$, NS $P > 0.1$). The only instance of two days sequentially having very high numbers ashore was when the first large numbers of immature Puffins arrived at the colony on 19 - 20 May. The first similar instance on Dun, on 26 and 27 May during the 1977 breeding season, was also after the main influx of immatures on 24 May. (Fig. 3.15). Peaks in colony attendance on Dun in both incubation and nestling periods occurred on average every two to four days. (Incubation: Dense $\bar{x}$ = 3.0 ± 0.60 days, 9 peaks; Sparse $\bar{x}$ = 2.56 ± 0.65 days, 9 peaks, 23 days' observation. Nestling: Dense $\bar{x}$ = 2.46 ± 0.40 days, 13 peaks; Sparse $\bar{x}$ = 3.75 ± 0.75 days, 8 peaks; 34 days observation.) There were no significant differences in the frequency of peaks between these two periods for either Sparse or Dense areas.

The number of birds flocking in the water was positively correlated with the number of birds later seen wheeling ashore at the Burrian area (r_s = 0.836, $P < 0.0001$) (Fig. 3.16). For the Sparse area on Dun, water flock numbers were also positively correlated with local wheel numbers (r_s = 0.615, $P < 0.001$) (Fig. 3.17). Numbers of birds in the water tended to be smaller off the Sparse area than off the Dense area, but numbers in the two areas were positively correlated (Fig. 3.18). This illustrates how water numbers gave

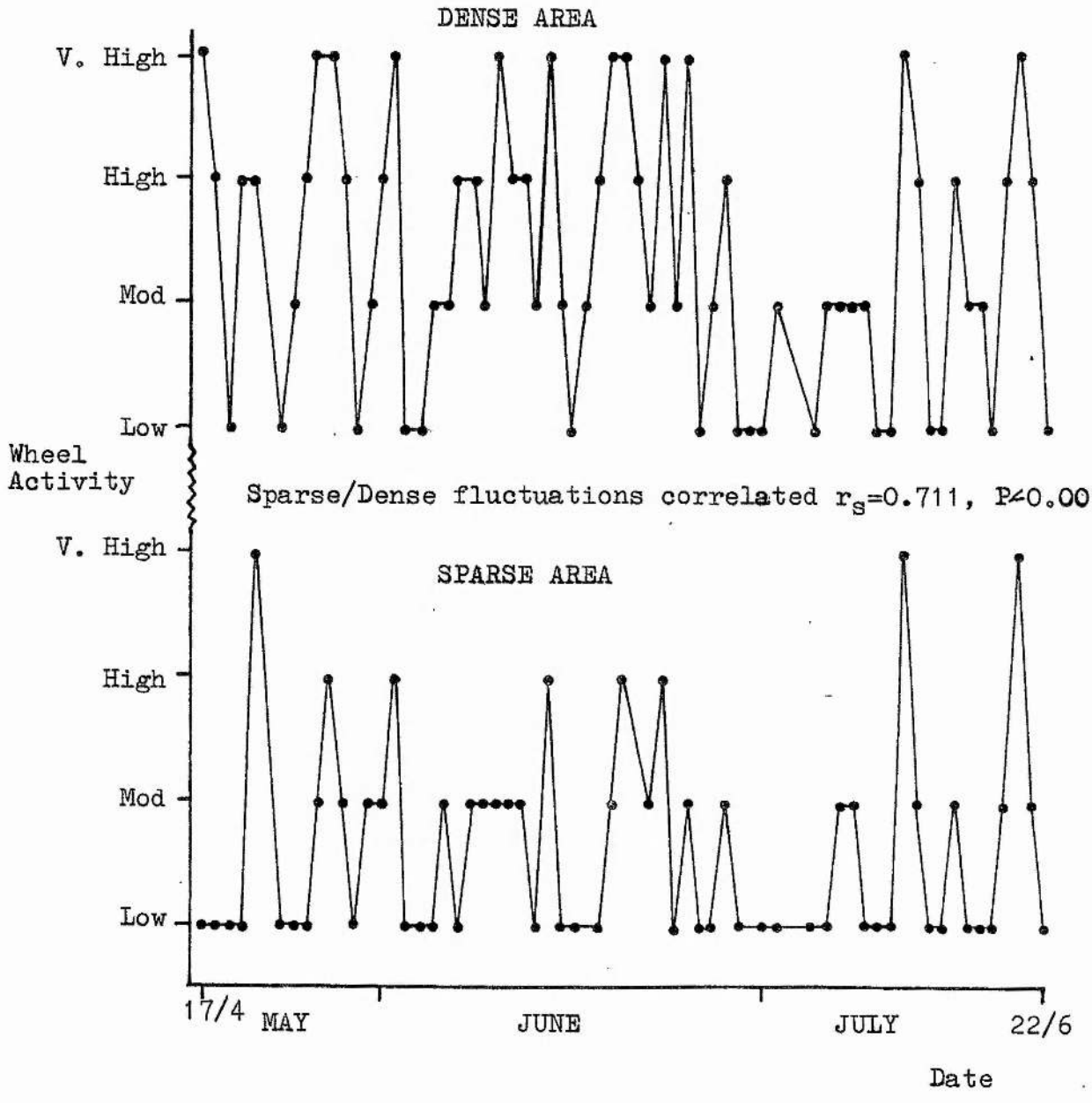


Fig. 3.15 Fluctuations in Dun wheeling activity, May-July 1977

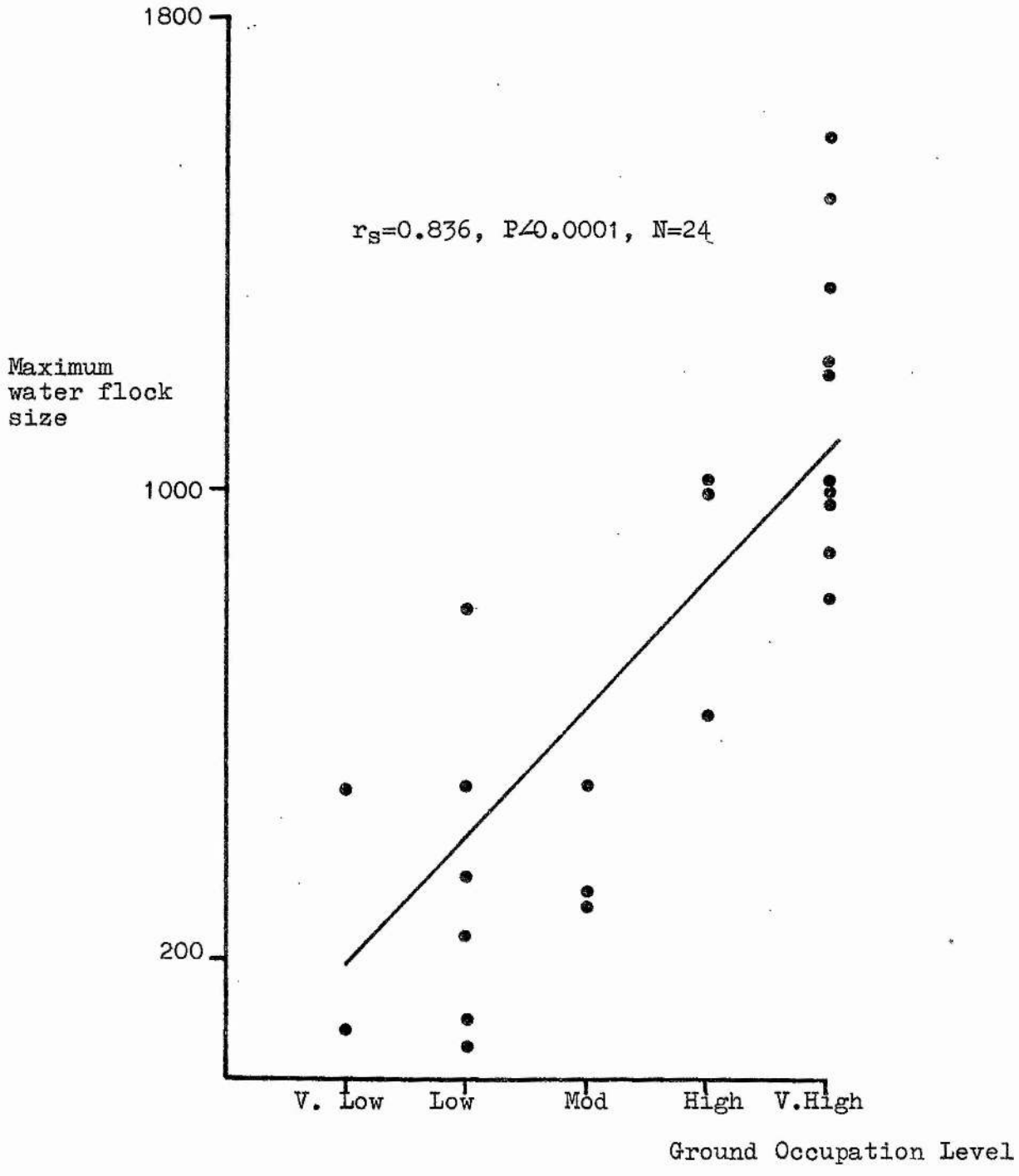


Fig. 3.16 Water flock size and ground occupation level, Isle of May, April-May 1978

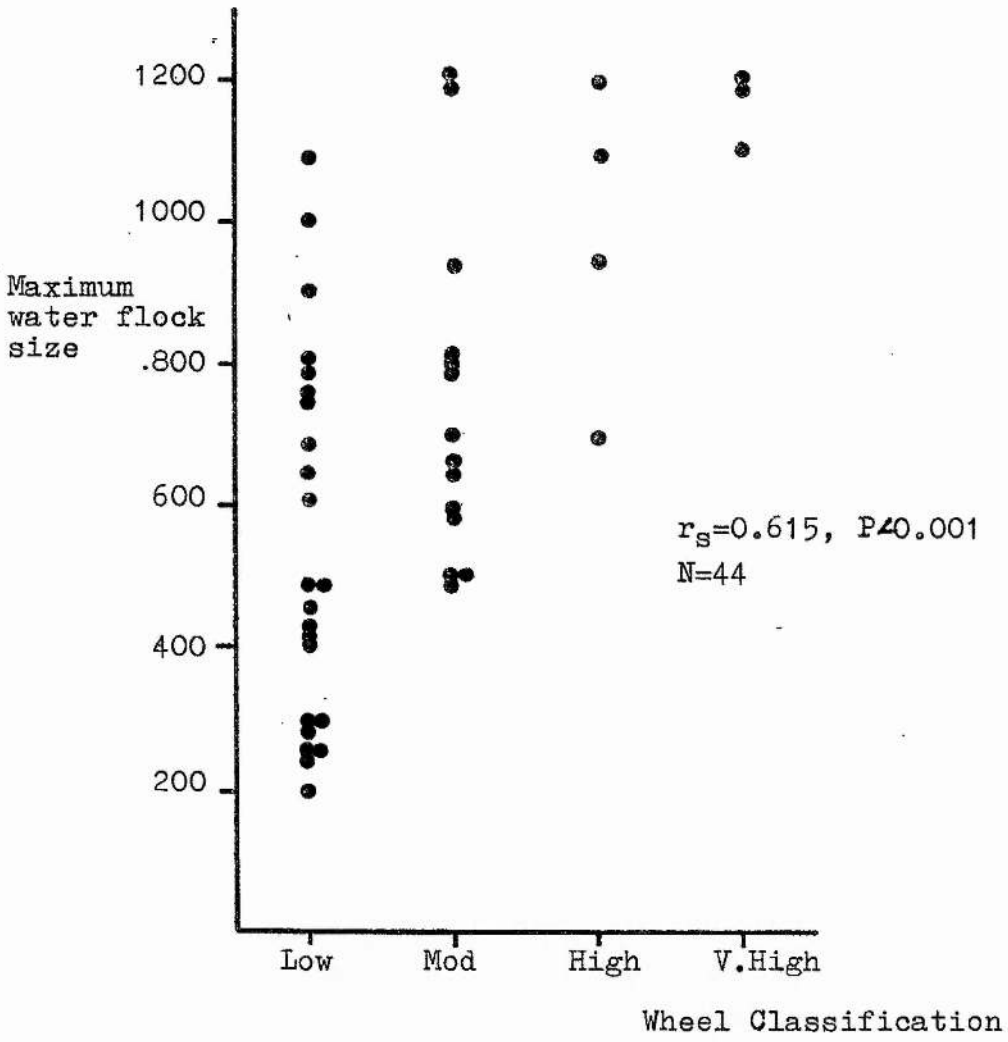


Fig. 3.17 Water flock size and wheel activity, Dun Sparse Area, 17/4 to 20/6/77

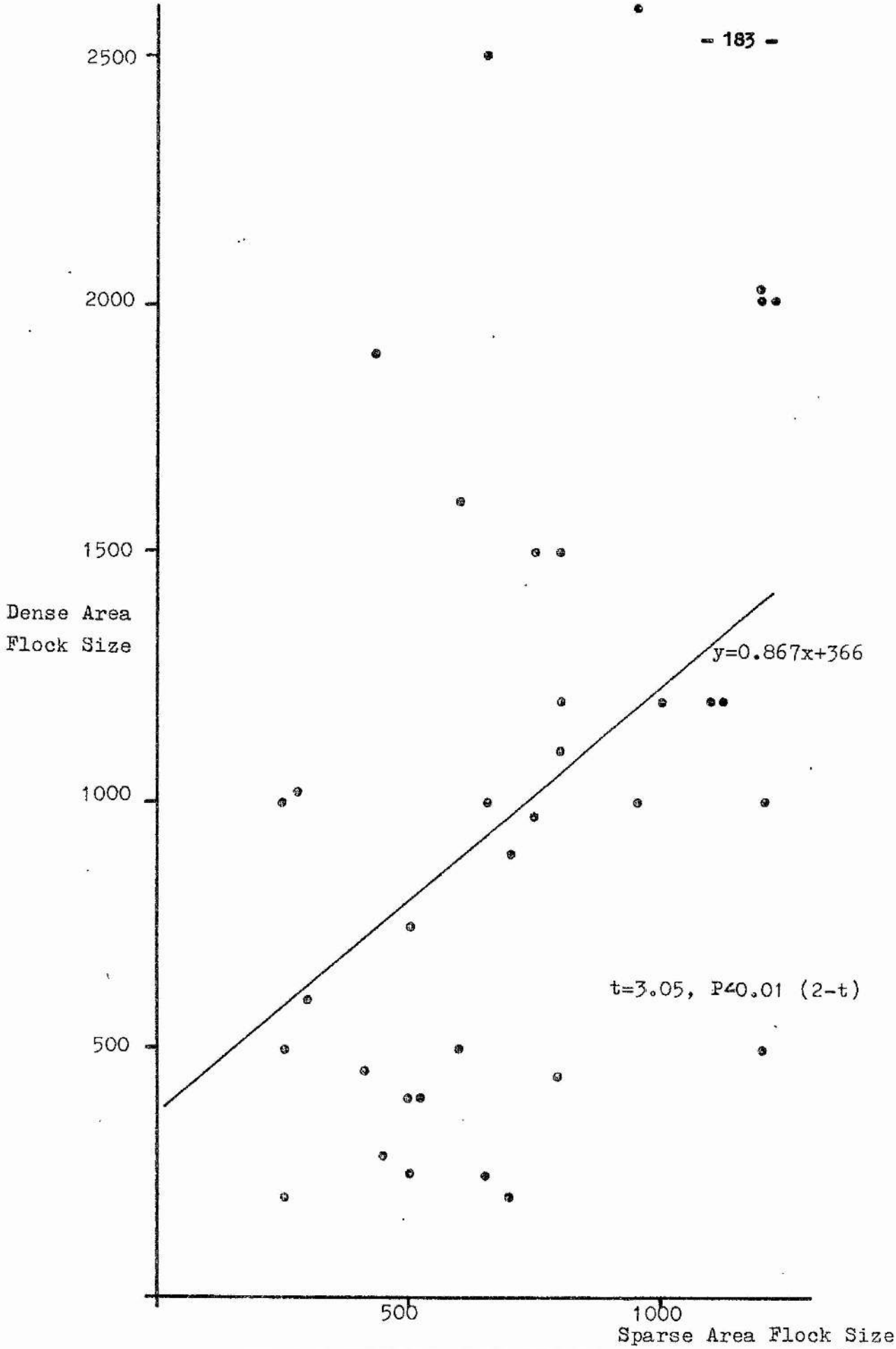


Fig. 3.18 Number of Puffins in water flocks off Dun, 17/4 to 11/7/78

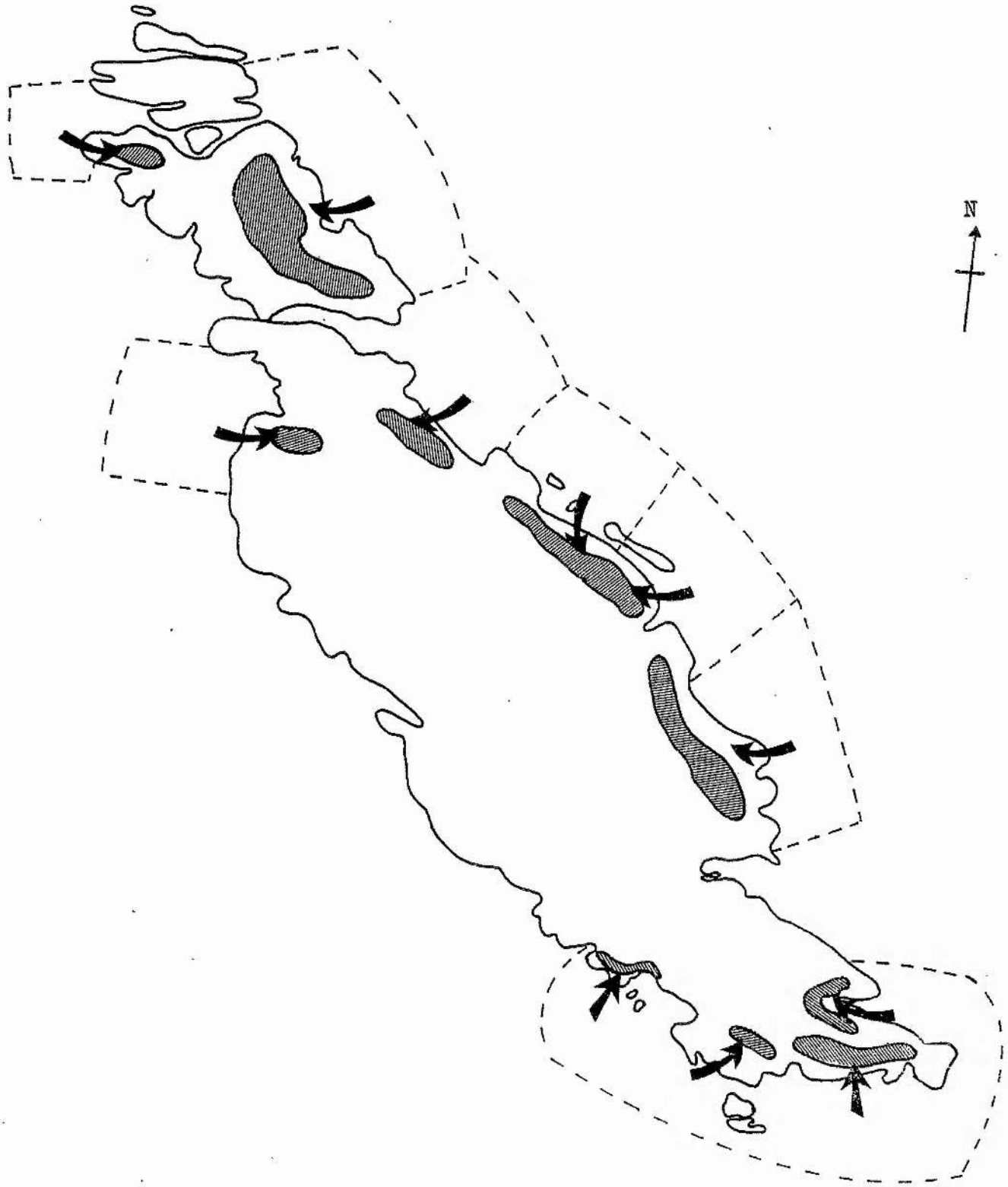


Fig. 3.19 Water grouping zones off main Isle of May Puffin sub-colony areas, 1977 and 1978

a crude index of the size of adjacent colony areas. Wheeling activity over both Sparse and Dense areas varied greatly from day to day, but again classifications of wheel numbers relative to the two areas were positively correlated.

Although water groups intermingled, birds tended to swim to and fro in a small area. For example, a bird landing off the Burrian was unlikely to swim farther than the sea area adjacent to the Burrian. By observing the patchy distribution of water groups resulting from this behaviour, and movements of birds from water flocks to colony areas, the rough extent of water flock zones associated with different colony areas was sketched (Fig.3.19).

Discussion

At least in the early stages of colony occupation in the pre-laying period, Puffins did not fly directly in to the colony from far out to sea. First arrivals at the colony initially grouped offshore. This is indicated by the correlation between water flock numbers and later wheel numbers. Once water flock numbers built up, the birds' behaviour changed, as indicated by the increase in flight intention behaviour such as Rise-up wing flapping.

Birds overflying water flocks usually tracked in to fly over land at the colony only when large numbers of birds from large water flocks took off from the water to join the flight. This is indicated by the data for 25 April 1978, where, with relatively low numbers of birds in the water off the Burrian colony, group merger was followed by water overflying but not by wheeling. Although numbers of birds present at

different colony areas were positively correlated, landfall at different areas did not necessarily occur at the same time. Thus, Puffins did tend to synchronise their movements to the colony with large numbers of other Puffins. This synchronisation occurred in small areas of the colony and was associated with wheeling over these areas. Numbers of wheeling birds increased around dusk, when birds were beginning to move from the colony to roost farther out to sea. Wheeling was thus associated with the synchronised movement of large numbers of Puffins, both to and from the colony. Sections following present data on the structure and distribution of wheels to investigate how wheeling might help individual Puffins synchronise their movements with other Puffins.

3.2 THE FORM AND DISTRIBUTION OF WHEELS

The temporal pattern of wheeling indicated that this behaviour was associated with movements of Puffins to and from different areas within a colony. The association between wheeling and different areas of a colony was also reflected in the spatial distribution of wheels. A wheel has four gross sections - an outer track, which is usually either over the sea or nearest the sea; an inner, over land track, and two turn regions where birds fly from outer to inner tracks and vice versa. At any one time, the Puffins flying in a single section fly in the same direction. Birds on the outer track fly with the wind, and birds on the inner track fly into the wind. (This feature of wheeling is well known to Faroese Puffin catchers on Mykines, who use

different sites for catching wheeling Puffins in different wind directions (Nørrevang 1977)). The polarisation of Puffins in outer and inner wheel sections is illustrated by photographs of a Dun wheel (Plates 3.1, 3.2).

Although the flight direction of Puffins within a wheel varied according to wind direction, the spatial extent of a wheel varied little throughout the breeding season. Maps of wheels over the Isle of May and Dun show the distribution of wheels there in 1977 and 1978 (Figs. 3.20; 3.21). These maps illustrate how birds turning out to the over sea track of one wheel were often near birds flying in the opposite direction in the turn region of an adjacent wheel.

Also, birds flying in wheels at different levels of the same slope sometimes flew in different directions when wind strength was low. This was noted for example in wheels over the Dense area summit slope on Dun and in wheels near Mykines village. Sketches of wheels over this area of Mykines illustrate how on one evening of slight wind, birds in the uppermost wheel above the Dalid colony area flew north→ south, whereas birds in the lower Dalid wheel flew south→ north (Fig. 3.22). Turn regions were often associated with topographic features such as land gullies, sea inlets and cliff promontories, but also occurred where there were no such features.

Inner wheel tracks reflected the distribution of burrows under the wheel. This was particularly obvious on Mykines, where burrows occur in the lower part of slopes near the cliff edge, with an abrupt boundary to burrow areas some tens of metres upslope from the cliff (Plate 3.3, and see

Fig. 3.20 Isle of May wheel tracks, 1977 and 1978

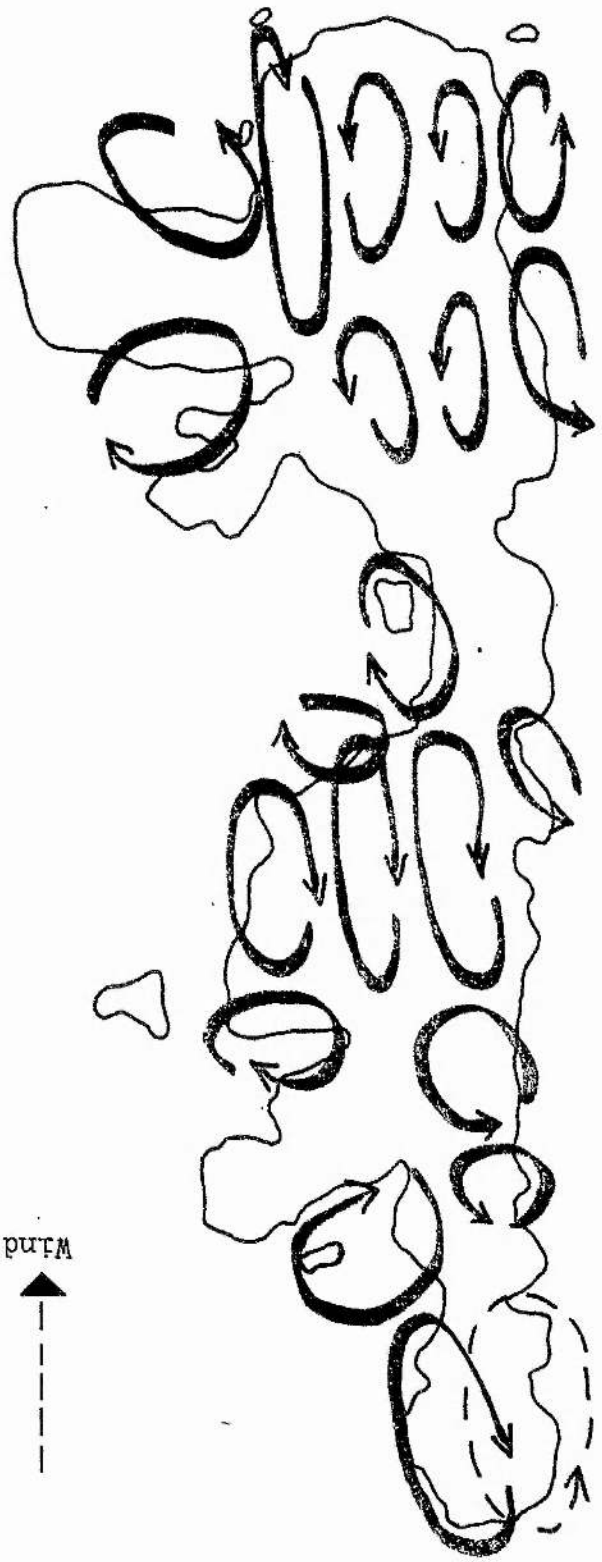
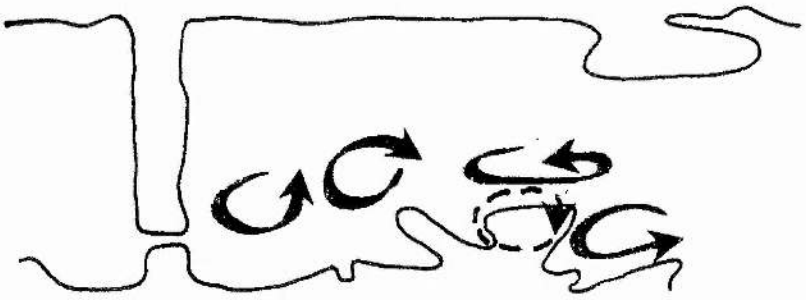


Fig. 3.21 Dun wheel tracks, 1977 and 1978

PLAN



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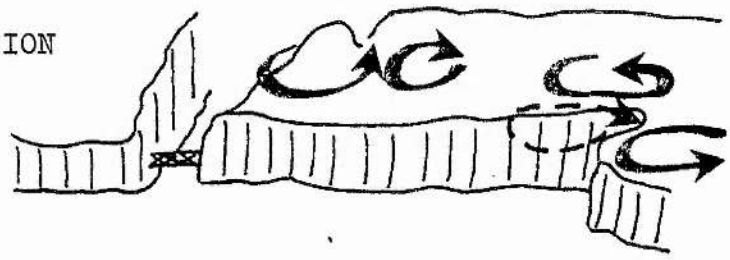


Fig. 3.22 Wheels near Mykinesbygd, 20.30 GMT 21/7/79

Plate 3.3 Boundary of Puffin sub-colony on Mykines

Nørrevang 1960). Here, the upslope limits of burrow areas were also the limits of inner wheel sections. This association of burrow areas and wheel dimensions was also noticeable on the Isle of May for the area immediately west of Holyman's Road. Wheel tracks over three distinct clusters of breeding sites at an Arctic boulder beach Puffin colony touched land precisely at the locations of breeding sites (Fig. 3.23).

Discussion

Wheel tracks in the air reflected the underlying distribution of breeding sites on the ground. Spatial association of wheels and breeding areas did not mean that the number of burrows was correlated with the number of wheels. For example, less than 100 pairs of Puffins bred at each of the three sites mentioned on Grimsey, and there were three different wheels associated with these sites. Over 12,000 pairs on the Dun Dense area summit slope also formed three wheels.

Puffin burrows are not distributed evenly throughout the colony. Topographic features such as rock gullies often separate different areas of burrows, as do less obvious habitat features such as patches of thin soil cover. To the human observer, a Puffin colony thus often appears to comprise a number of burrowed sub-areas. A sub-area map of the Dun colony, based on the type of features described here was produced by Harris and Murray (1977) (Fig. 3.24). The map of Dun wheels is broadly similar to this map of human classified colony sub-areas. This suggests that the dis-

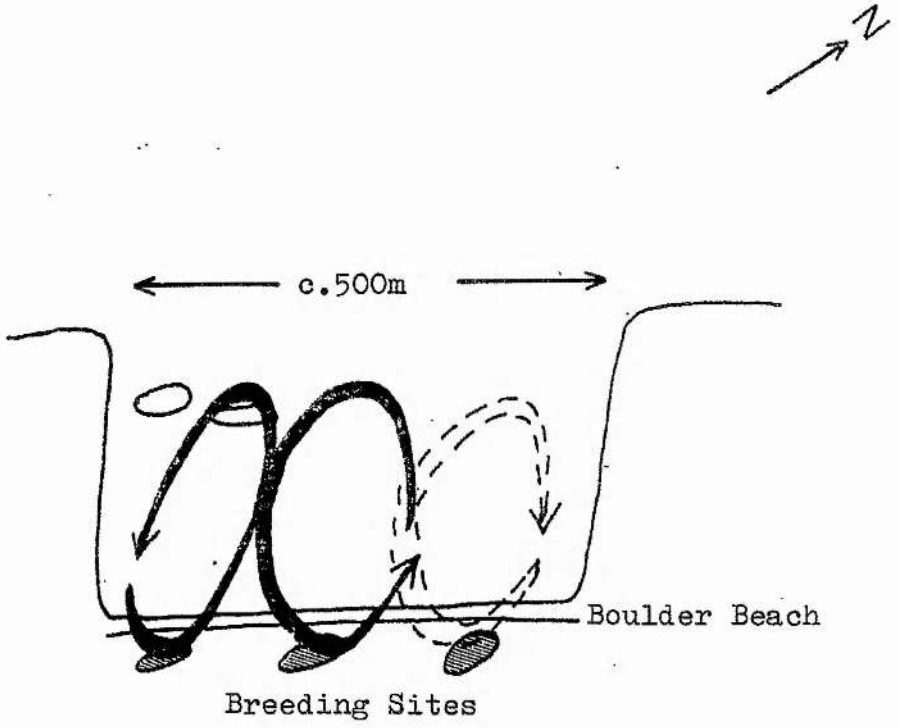


Fig. 3.23 Wheels near Arctic boulder beach Puffin breeding sites, Grimsey, 21.00 GMT 4/8/79

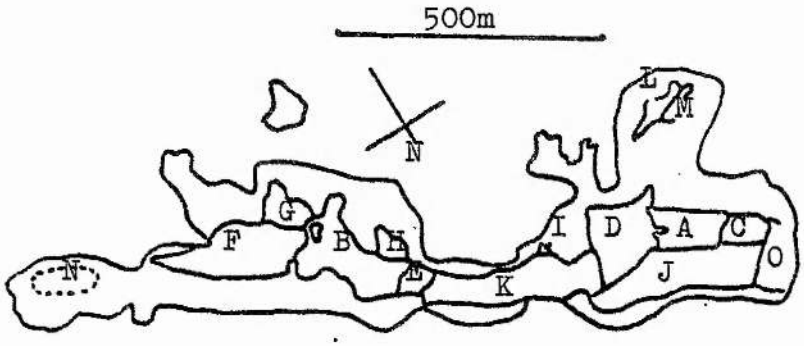


Fig. 3.24 Main Puffin sub-colonies on Dun identified in 1975 (from Harris and Murray 1977)

continuous distribution of burrows on the ground is also perceived by the Puffins themselves. The number of birds potentially participating in any one wheel is thus a function both of underlying burrow density and of sub-colony area, this area being a function of discontinuities in the habitat.

3.3 BEHAVIOUR OF PUFFINS IN A WHEEL

An individual Puffin flying in a wheel could behave in a number of different ways other than flying repeated circuits of the wheel track. It might land without flying a complete circuit of the wheel track, leave the wheel to join another wheel, or leave the wheel to fly down to the sea. It might also fly a course which involved more aerial turns than the normal elliptical wheel track. The most commonly observed course deviation was where a Puffin flew in a loop from one part of the wheel, out and back in to the wheel track near the point where it had started the extra turn. This type of behaviour is referred to here as 'looping'. Less often, one or more Puffins would plummet from one part of a wheel to a lower attitude, either continuing to fly in the wheel track after this, or dropping down towards the sea. These different behaviour classifications are used in the analyses presented here.

Behaviour in the absence of hunting gulls

There was no significant difference in the mean time taken by birds in areas of different underlying burrow density to fly a complete wheel circuit if looped tracks are excluded

(Fig. 3.25). Timings are for birds flying under similar low wind conditions of Beaufort Force Three or less. The flying speed of wheeling Puffins in low wind, taken from stopwatch timings of birds flying over landmarks, was around 60 Km/hr. (2 areas. First, $\bar{x}$ = 58.10 ± 1.45 Km/hr, N = 9 birds; Second, $\bar{x}$ = 62.60 ± 3.59 Km/hr, N = 12 birds).

Looped tracks were of significantly longer duration than unlooped tracks (Table 3.9). The mean track duration for any one wheel was thus, not surprisingly, positively correlated with the percentage of individuals observed which looped (Fig. 3.26). Birds looped significantly more over low burrow density areas than high density areas (Fig. 3.27). This is a reflection of the different numbers of birds participating in wheels over areas of different burrow density. The association between looping and the number of birds in a wheel is illustrated by data on single wheels (Table 3.10). With similar numbers of Puffins in a wheel in different observation periods, a similar percentage of birds looped. With lower numbers in the wheel, significantly more birds looped. This meant that mean wheel track durations were similar when wind and wheel number conditions were similar, as illustrated by data for a wheel over Dense area E on two different days (Fig. 3.28).

The number of loops made by a bird in a single wheel circuit was random, as judged by the fit of the observations to an expected Poisson distribution (χ^2 = 0.046, 1df, N = 46 birds).

Individual birds did not necessarily loop on every wheel circuit. For birds in Dense area wheels, 65% of loops in non-hunt periods were followed by the bird leaving the wheel

Table 3.9 Wheel duration ± loops

Area	$\bar{x}$ unlooped wheel duration	$\bar{x}$ incl. looped duration	% looped
J	20.4 ± 3.9	21.2 ± 5.4	5.9
A	20.0 ± 3.4	36.4 ± 13.8	17.0
E	19.8 ± 3.0	20.0 ± 3.1	3.3
F east	18.9 ± 2.9	19.2 ± 3.5	4.3
F west	18.8 ± 3.5	20.3 ± 5.8	10.9
B north	20.6 ± 2.2	20.9 ± 2.9	2.9

Sign test, $\chi = 0$, $p < 0.05$

Table 3.10 % Wheel tracks looped and number of Puffins in wheel, Dun

Area	Puffins in wheel	% looped	% unlooped	N	χ^2	p
A	Mod	15	85	39	0.24	NS
	Mod	17	83	53		
	Low	58	42	48	28.19	< 0.001
J	Mod	6	94	68	33.04	< 0.001
	Low	49	51	59		

Table 3.11 % Wheel tracks looped and local wind conditions

Day	Area	Puffins in wheel	Wind	% looped	% unlooped	N	p
14/4/80	N.Colm	Mod	E.4-5	92	8	100	< 0.001 (χ^2)
	Bishop	Mod	(sheltered)	4	96	23	
16/4/80	N.Colm	Mod	(sheltered)	-	100	17	1.13^{-11} (Fisher exact)
	Bishop	Mod	WNW4	100	-	23	

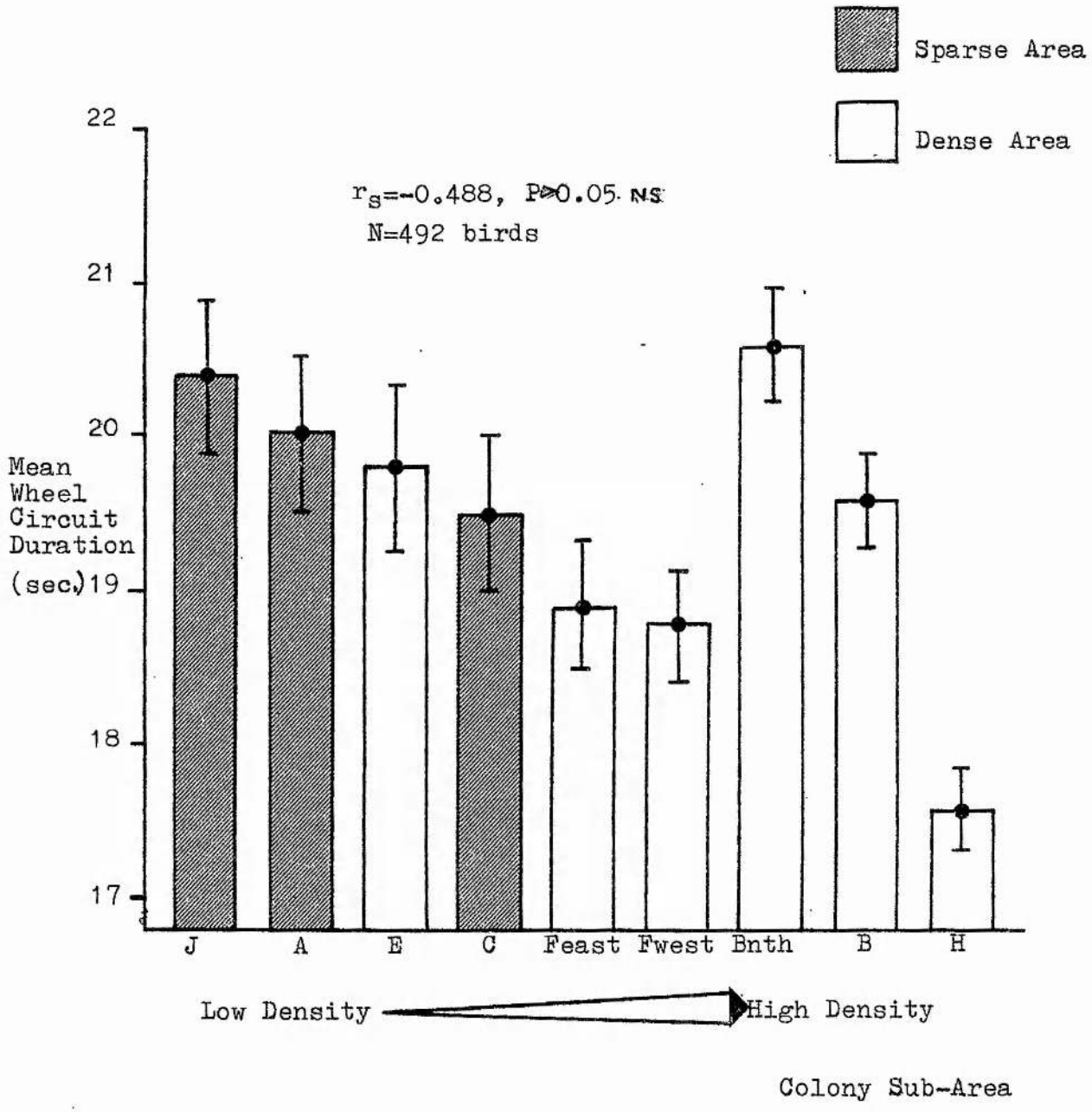


Fig. 3.25 Mean duration of single wheel circuits by individual Puffins in wheels over different sub-colonies on Dun (see Fig. 3.24 for sub-area key)

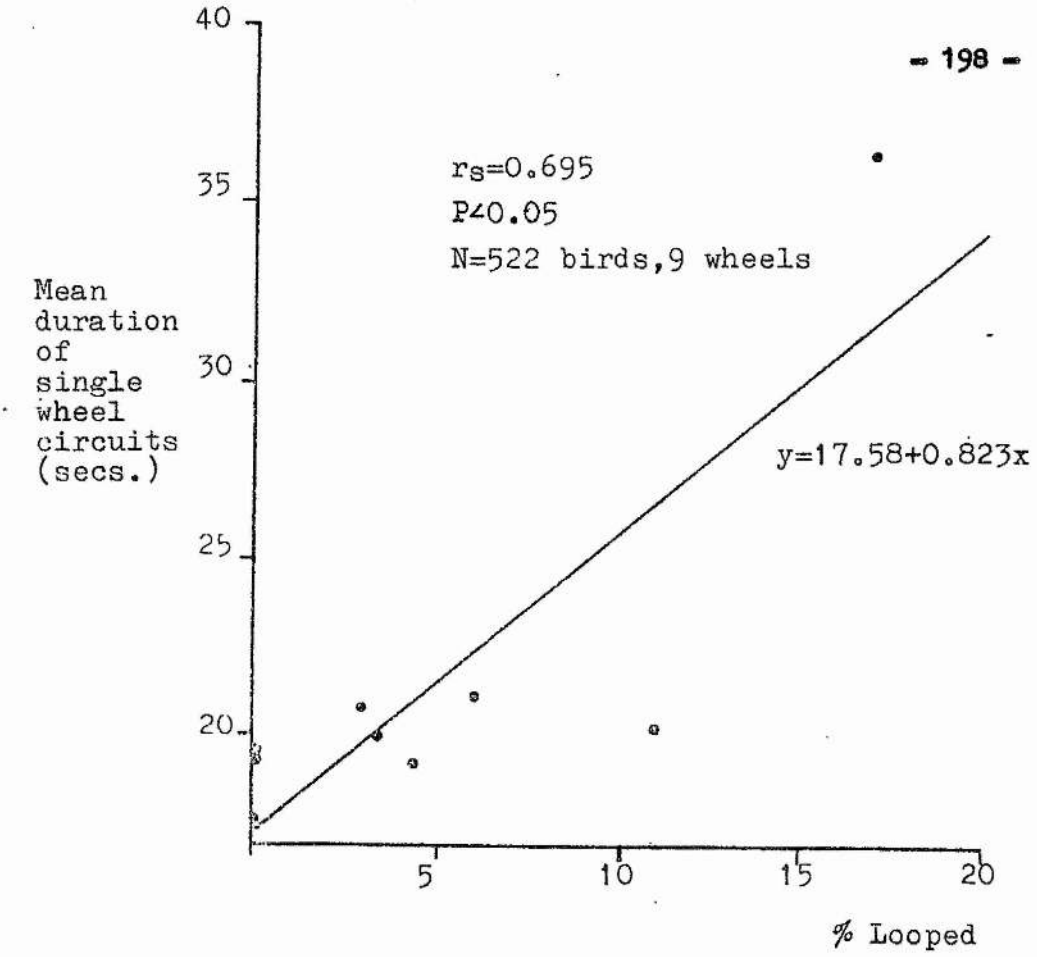


Fig. 3.26 Mean duration of wheel circuits by individual Puffins and percentage circuits looped

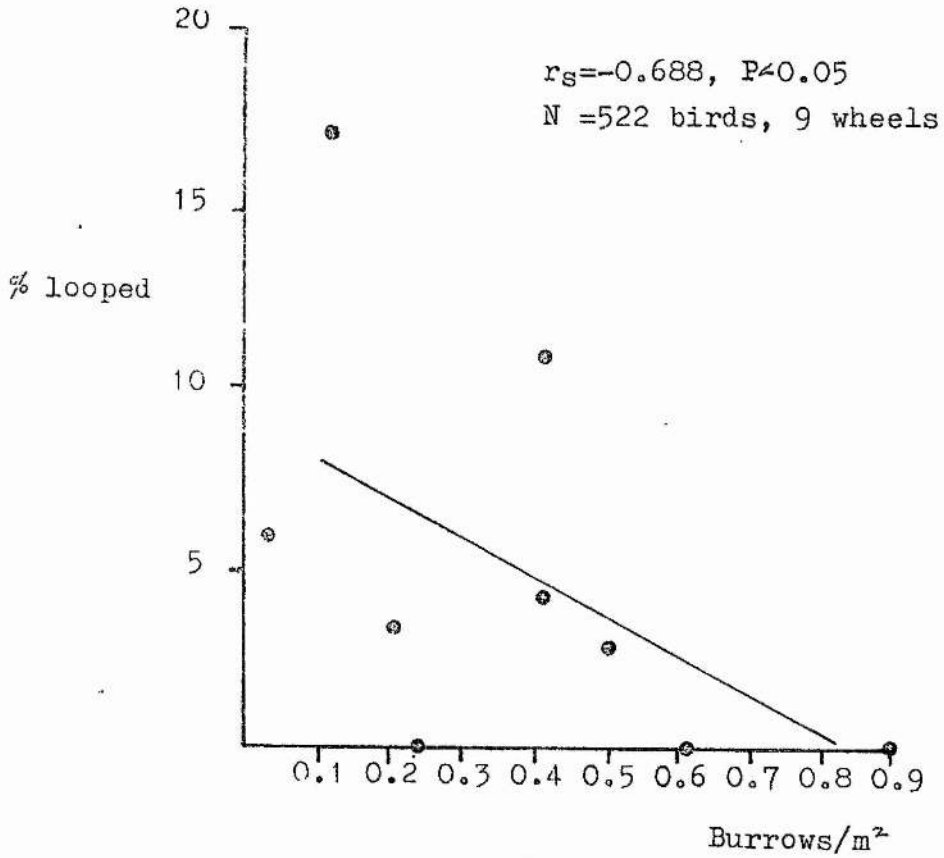


Fig. 3.27 % Wheel circuits looped and burrow density under wheel

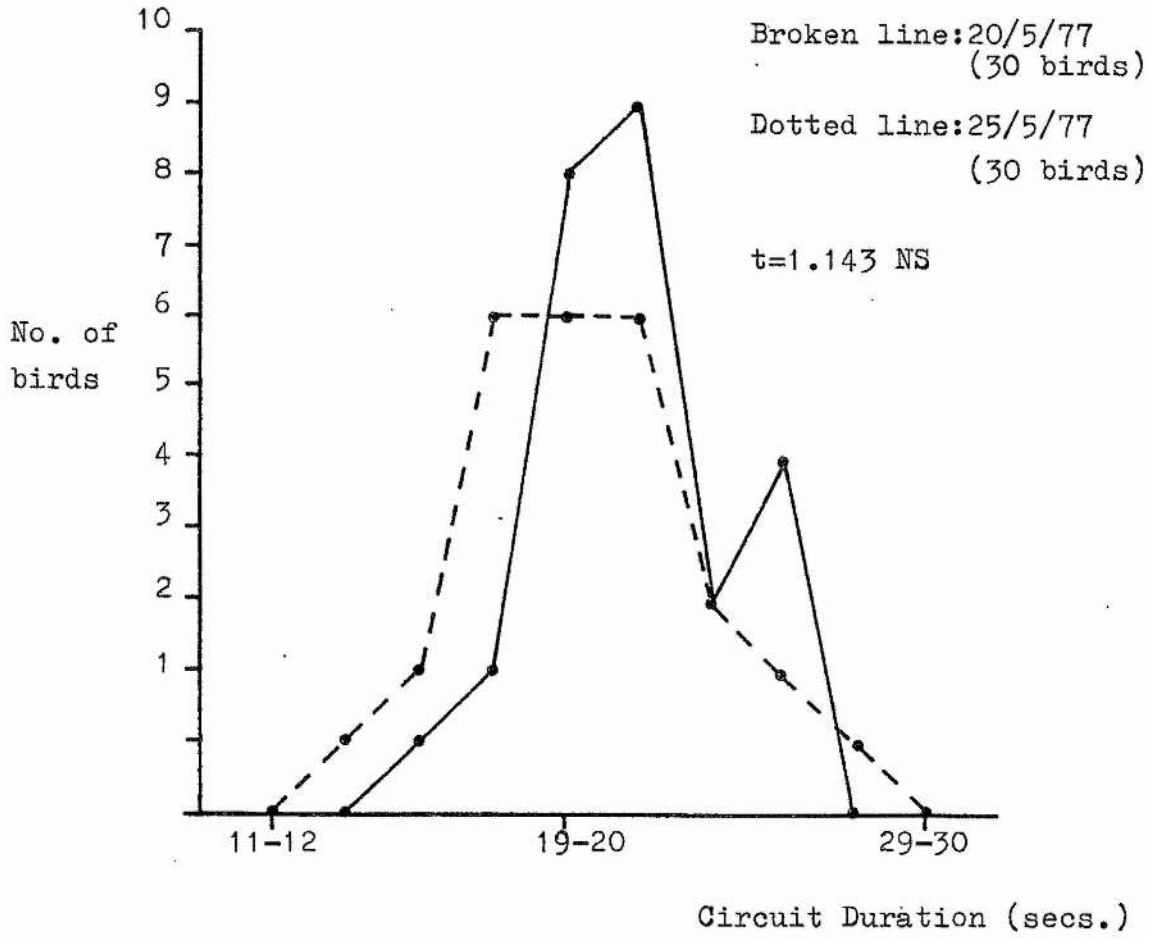


Fig. 3.28 Distributions of wheel circuit durations on two different days in the same sub-colony area (non hunt periods)

in the same or next circuit. This was not the case for Sparse area birds, 78% of which stayed in the wheel for at least one further circuit after looping, significantly different from Dense area birds ($\chi^2 = 2.2$, $p < 0.0005$, 1-t, $N = 137$). The looping behaviour of 15 birds in two Sparse and Dense colony areas illustrates this difference (Fig. 3.29).

When wind strength was force four or more, more birds looped. This is illustrated by data for two areas on the east and west sides of the Isle of May (Table 3.11). Birds wheeling at the Bishop were relatively sheltered from an easterly wind, whereas birds wheeling at the Colm area were exposed, and vice versa for a westerly wind. The table illustrates the effect of wind on looping between the two areas on the same day, and within the two areas on different days.

In strong winds of force six or more, the flight pattern of Puffins in a wheel area changed drastically. The birds tended to be bunched in one flock which flew in tight zig-zag tracks, overshooting the normal wheel boundaries. This was largely due to birds being hurtled in one direction by the wind turning to fly back into the wind being visibly difficult. The influence of wind strength on flight behaviour is illustrated schematically in drawings based on observations made at the Burrian area on the Isle of May (Fig. 3.30).

70% of birds in Dense area wheels used the same turn regions on successive circuits, significantly different from Sparse area birds, 51% of which used different turn regions

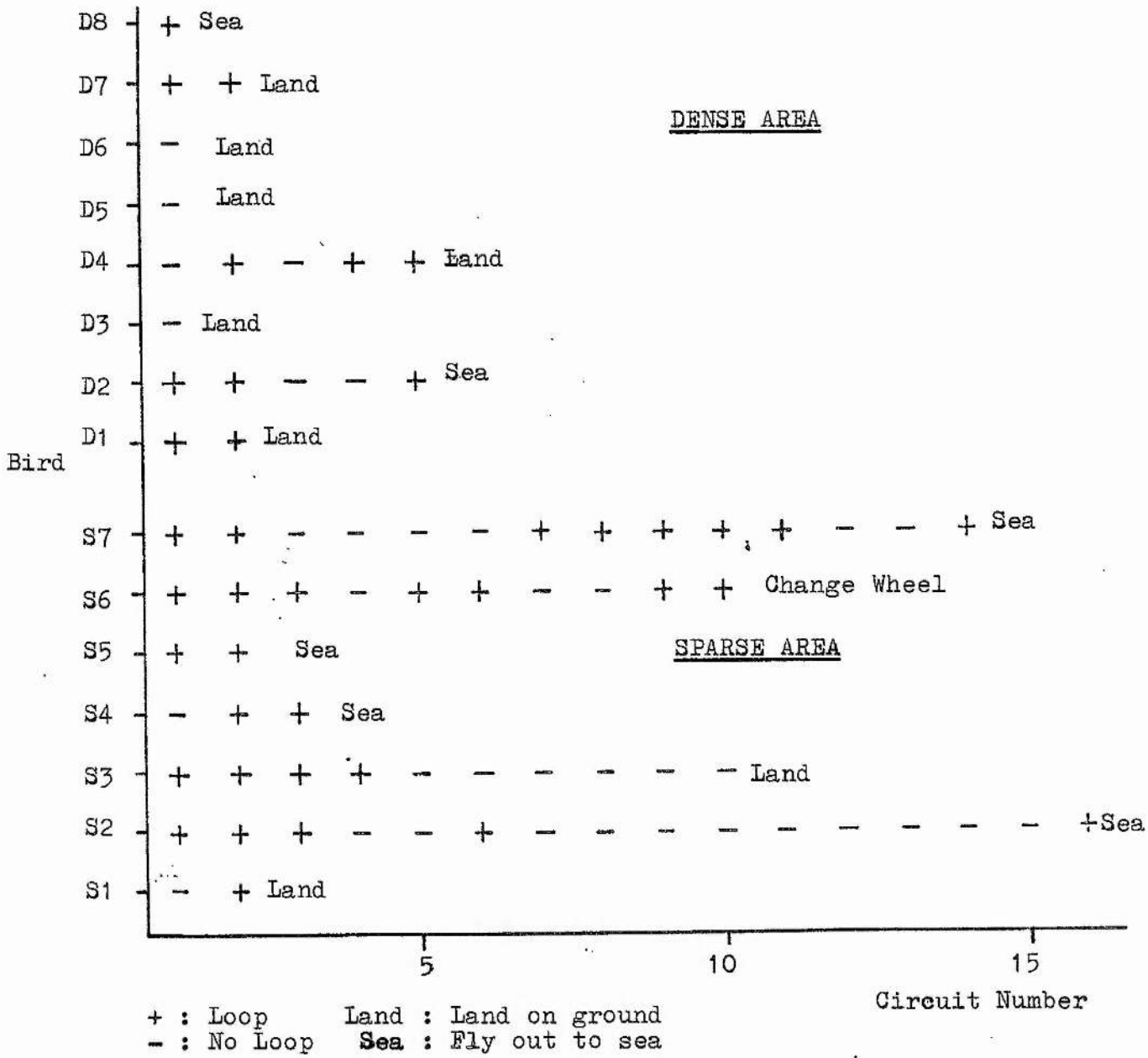


Fig. 3.29 Looping behaviour of individual Puffins in wheels in Sparse and Dense Areas

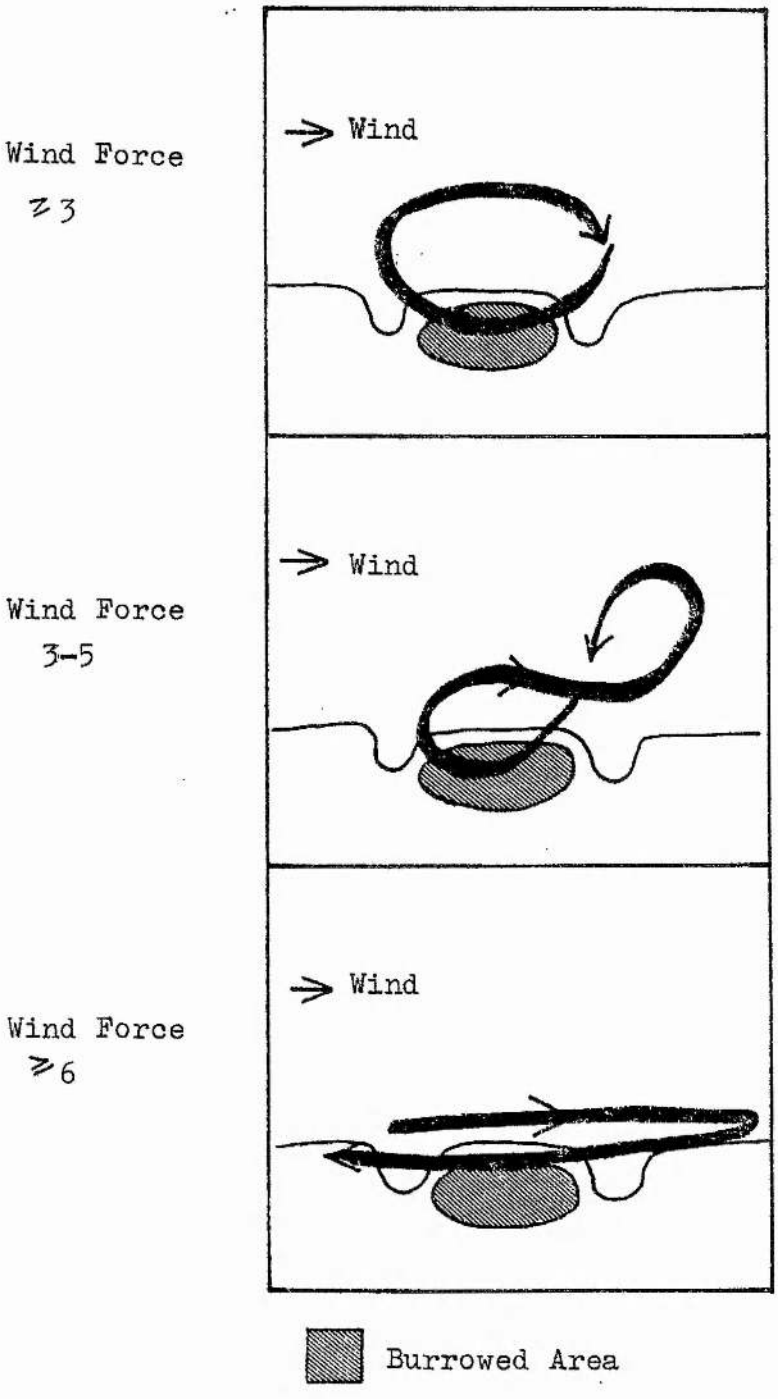


Fig. 3.30 Flight paths of Puffins in a wheel under different wind conditions

on successive circuits (χ^2 = 11.06, $P < 0.0005$, 1 - t, N = 238). This difference was reflected in the sequential circuit times of Dense area birds being less variable than those of Sparse area birds (Fig. 3.31), although there is insufficient data for the Sparse area to test the significance of this difference. For timings of different birds monitored for only one wheel circuit there was no significant correlation between unlooped wheel circuit variance and burrow density under wheels (r_s = -0.388, NS $p > 0.05$, N = 496 birds).

An individual Puffin usually only participated briefly in a wheel, making on average one to two wheel circuits before leaving the wheel ($\bar{x}$ = 1.56 $\pm$ 0.15 circuits, N = 168 birds, Areas B, G, H and E). The majority of birds landed at the colony in less than or equal to one circuit (61.31%, N = 168 birds). Five percent left the wheel to fly down to the sea, all birds which landed in the sea landing in an area immediately offshore from their previous wheel area (N = 34 birds). Five percent left the original wheel to fly in another wheel (N = 685 birds). There was no difference in the frequency of departures from wheels between Dense and Sparse areas. (All χ^2 comparisons $P > 0.05$, N = 685 birds).

Fish carriers made significantly fewer wheel circuits before landing at the colony than birds without fish (χ^2 = 10.39, $P < 0.005$, 1 - t, N = 800 birds). (Table 3.12).

The number of wheel circuits flown by birds without fish before landing had a negative exponential distribution (Fig. 3.32). ($\hat{k}$ = 0.7135, χ^2 = 1.47, p = 0.48 for match between observed and expected frequencies, N = 99 birds).

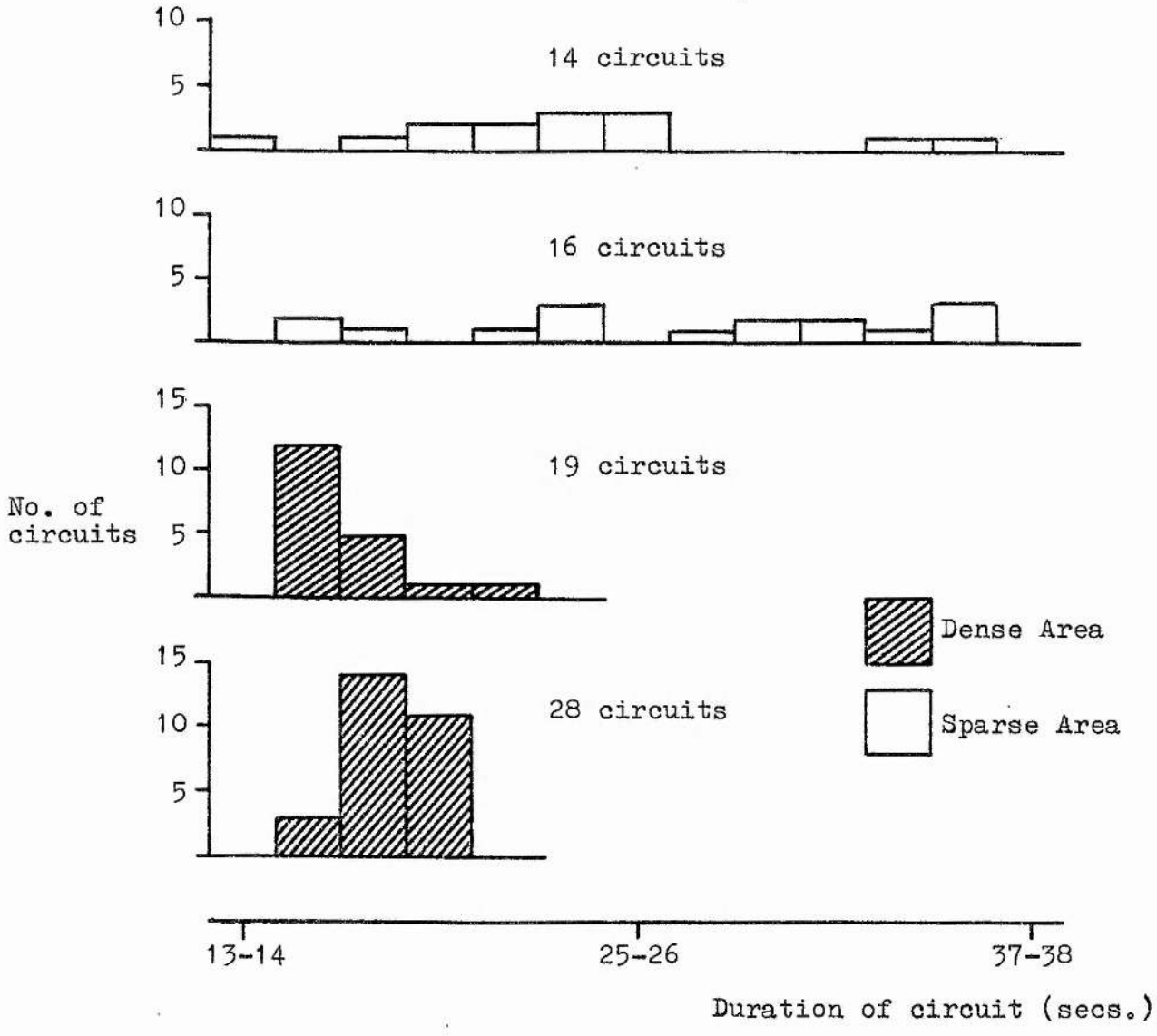


Fig. 3.31 Duration of wheel circuits flown by four individual Puffins, Sparse and Dense Areas

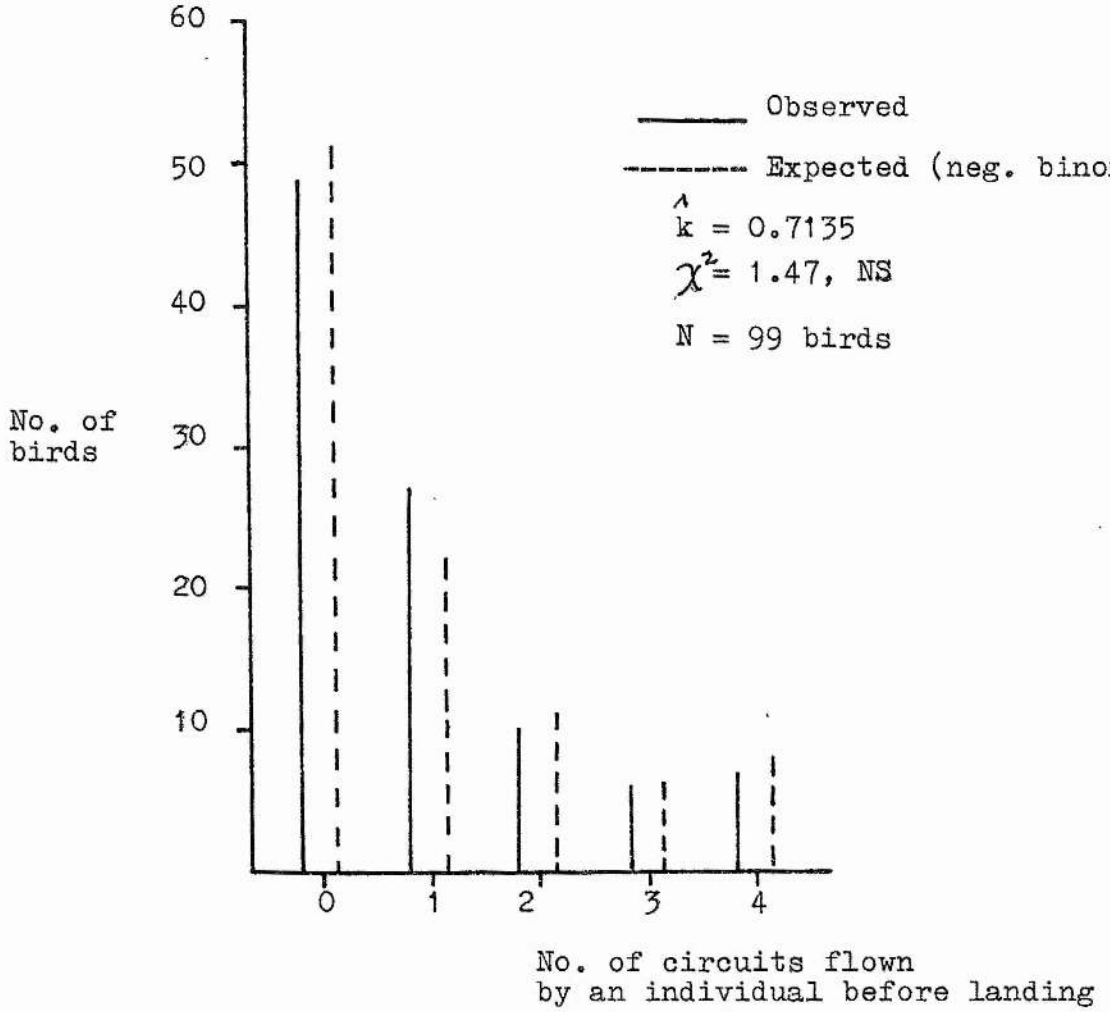


Fig. 3.32 Number of wheel circuits flown by individual Puffins (not carrying fish) before landing at Dense Area G : observed and expected (negative binomial)

Table 3.12 Number of wheel circuits flown by Puffins before landing at the colony

Birds/ No.of circuits	No Fish	Fish Carrier	
≤ 1	220	35	255
>1	507	38	545
	727	73	800

χ^2 = 10.39, $p < 0.005$ 1 - t, n = 800 birds

Table 3.13 Land flight focus of wheelers tracked from over sea to slope

Sea \ Slope	Top	Mid	Low	N
High	11	1	-	12
Mid	2	12	3	17
Low	1	1	15	17
	14	14	18	46

Table 3.14 Landing area of wheelers tracked from over sea to slope

Sea \ Slope	Top	Mid	Low	N
High	2	-	-	2
Mid	-	7	-	7
Low	-	1	7	8
	2	8	7	17

A Puffin's outer wheel track position corresponded closely with its inner wheel track position and with the part of the colony slope where it later landed (Tables 3.13, 3.14). That is, a bird flying high in the outer wheel track tended to fly high on the inner track and to land high up the colony slope.

To summarise, in the absence of hunting gulls the behaviour of a wheeling Puffin was influenced by the number of other Puffins in the wheel, by wind strength and by whether the Puffin carried fish or not. Increasing wind strength and decreasing numbers of Puffins in a wheel area were both associated with individual birds often making looped turns in a wheel circuit. Single Puffins made only a few circuits before leaving the wheel, most departures being followed by landing at the colony. Birds tended to land at an area of slope immediately under their previous wheel track, and fish carriers landed after fewer wheel circuits than birds without fish.

Discussion

If it is assumed that when wind is slight wheeling Puffins fly at roughly the same speed in different areas, the similarity in unlooped wheel circuit times for different Dun wheels indicates that each wheel encompassed a similar ground area under its track. The majority of Puffins in a wheel burrowed in or otherwise used the colony area immediately under that wheel. The number of Puffins potentially participating in a wheel will thus be a function of underlaying burrow density. The number of wheels will be independent of burrow density, being rather a function of colony area.

The similarity in the number of wheels over Dun and the Isle of May, two islands of similar size but vastly different Puffin population, further suggests this type of relationship. Counts of wheeling Puffins could thus give a means of estimating the numbers of Puffins breeding at sites where burrows are inaccessible, such as talus slopes or boulder beaches, an important habitat for Puffins north of Britain. Baseline data could be provided by counts of wheeling birds over areas where burrows are accessible. Together with counts of birds in water flocks off the colony, such data may allow more accurate censusing of Puffin populations throughout the species' range than has been possible to date.

Looped wheel tracks in periods of strong wind have been described for Puffins at Norwegian and Russian colonies (Skokova 1962, Myrberget 1962).

The tendency for Puffins to loop more frequently when small numbers of birds were in a wheel, or with strong winds, suggests that looping may be an attempt by single birds to fly close to others. Looping could allow a Puffin to see birds flying behind it in a wheel, and hence assist aerial grouping when wheel birds are few or fragmented. The erratic wheeling behaviour of Sparse area birds relative to Dense area birds also suggests that wheels with few Puffins are less structured than wheels with large numbers.

It is impossible to prove the assumptions behind a statistical distribution true by successfully fitting the distribution to a set of data (cf Poole's discussion of the negative binomial distribution (1974)). The fit between

observed and expected frequency distributions can nevertheless suggest processes which result in the observed pattern. The distribution of the number of wheel circuits made by Puffins before landing at the colony closely resembles a negative binomial distribution. Puffins often leave a wheel in groups. This results in landings at the colony being clustered in space and time (cf Ashcroft 1977). Such landing episodes may be initiated by a single wheeling bird, others following it rapidly. A contagious distribution of wheel circuits could arise if the chance that a bird starts a landing episode is random, but the number of birds following this leader increases logarithmically during the landing episode. These ideas could be investigated in the field. At present they suggest that individual Puffins tend to synchronise their departures from a wheel with other Puffins. Data presented in this section also indicates how wheeling behaviour itself could assist in aerial grouping of birds which later land at a colony area under a wheel.

3.4 WHEELING BEHAVIOUR IN THE PRESENCE OF PREDATORY GULLS

Gulls hunting in the vicinity of a wheel inhibited departures of Puffins leaving the wheel to land at the colony in both Sparse and Dense areas (Tables 3.15, 3.16). This was the case for both fish carriers and birds without fish ($\chi^2 = 0.22, P>0.5$ no difference in fish/no fish bird landings, N = 124 birds). Fish carriers made significantly more circuits before leaving a wheel in a hunt period than at other times ($\chi^2 = 37.06, P<0.0005$, 1df, N = 165 birds).

Tables 3.15, 3.16 Puffins landing from wheel in less than or equal to one circuit in presence and absence of hunting gulls

Sparse Area

	+ Hunt	- Hunt	
+ Land	5	23	28
- Land	67	73	140
	72	96	168

$\chi^2 = 9.84, P < 0.0005$, 1 - t

Dense Area

	+ Hunt	- Hunt	
+ Land	3	18	21
- Land	43	44	87
	46	62	108

$\chi^2 = 10.04, P < 0.0005$, 1 - t

There were also significantly fewer departures from wheels to the sea during hunt periods (Sparse area: $\chi^2 = 7.79, P < 0.01$, 2 - t, 2 df, N = 200 birds; Dense area: $\chi^2 = 7.34, P < 0.01$, 2 - t, 2 df, N = 392 birds).

Significantly more birds in both Sparse and Dense areas looped when a hunting gull was nearby than at other times (Sparse area: $\chi^2 = 8.42, P < 0.0005$, 1 - t, N = 130 birds; Dense area: $\chi^2 = 18.44, P < 0.0005$, 1 - t, N = 306 birds) (Tables 3.17, 3.18).

Birds which looped during hunt periods in the Dense area tended to stay in the wheel for at least one further circuit after looping, significantly different from birds which looped at other times ($\chi^2 = 32.97, P < 0.0005$, 1 - t, N = 207 birds). Changes in looping behaviour in the presence of a hunting gull and with changes in the number of wheeling Puffins are illustrated for a Sparse area wheel (Table 3.19).

Tables 3.17., 3.18. Looping behaviour in the presence and absence of hunting gulls

3.17. Sparse Area

	Hunt	No Hunt	
Loop	16	4	20
No Loop	46	64	110
	62	68	130

More looping in hunt periods, $\chi^2 = 8.42$, $P < 0.005$

3.18. Dense Area

	Hunt	No Hunt	
Loop	26	35	61
No Loop	40	205	245
	66	240	306

More looping in hunt periods, $\chi^2 = 18.44$, $P < 0.0005$

Table 3.19 Wheel looping with changing wheel strength and with presence of a hunting gull.
Dun, Low Sparse wheel

Wheel Strength	? Hunt	$\bar{x}$ Wheel (secs.)	% Loop	N
MOD	-	20.4 ± 3.9	5.9	68
MOD	+	20.0 ± 4.2	25.8	62
LOW	-	23.5 ± 6.5	49.2	48

Reaction to Gull Attack

Individual Puffins attacked by a gull reacted in different ways according to the nature of the attack. The majority of Puffins involved in class two encounters with a gull (near misses) stayed in the wheel after the attack, although they would normally plummet to a lower level of the wheel, or veer away from the attacking gull. This meant that a Puffin which had been narrowly missed by a gull would usually be back in the air space where the attack had occurred within half a minute after completing a further wheel circuit. Puffins which were caught by a gull and then escaped in the air, or which were chased by a gull out from a wheel over the sea, invariably left the wheel and landed, usually in the sea. Rarely, a Puffin dropped by a gull in the air left the wheel and ran down a burrow. The difference in Puffin behaviour after near misses and after dropped catches or prolonged chases was significant in the two observation periods where these aspects of Puffin behaviour were quantified (Fisher exact P = 0.00005, 1 - t, N = 17 encounters).

Small groups of less than ten Puffins sometimes plummeted to a lower level of a wheel, or dropped out of a wheel, when a hunting gull flew nearby. Individual birds in such groups matched the flight movements of other birds in the group, so that, for example, all the birds in such a group tended to turn in unison.

Discussion

In the presence of hunting gulls, Puffins stayed in a wheel longer than at other times. Departures from the wheel were often either when the Puffin was in serious danger of being caught, or conducted in unison with several other Puffins. The presence of an aerial predator thus appeared to increase an individual Puffin's tendency to remain in the air near other Puffins. That birds usually remained in a wheel even after being narrowly missed by a gull also suggests such a tendency - leaving a wheel in a hunt period may be a dangerous move unless the Puffin is already at serious risk. Looping behaviour has already been discussed in the previous section as a means whereby a Puffin could increase its chances of flying close to other Puffins in a wheel. Data on looping in the presence of a hunting gull follows the pattern which would be expected if looping in part served such a function. - It has already been shown that hunting gulls are 'confused' by large numbers of Puffins in a wheel. If bunches of Puffins within a wheel also confused a gull, flying near other Puffins in a wheel would be advantageous for individual birds. Hence, if looping assisted Puffins in flying near other Puffins, this behaviour might be expected to occur more frequently during hunt periods than at other times.

3.5 THE SPATIAL DISTRIBUTION OF PUFFINS IN A WHEEL IN THE PRESENCE AND ABSENCE OF HUNTING GULLS

Data presented in the previous section on the looping behaviour of Puffins wheeling in the presence of a hunting gull suggests that Puffins may attempt to fly closer to other Puffins during hunts than at other times. This section presents quantitative information on the spatial distribution of wheeling Puffins to examine this suggestion.

Methods

Data on the spacing of Puffins flying in hunt and no-hunt periods was obtained by photographing part of a single wheel over Dense area F during a sample of such periods in June 1980. All photographs were taken on a motor-driven Olympus OM-1 camera, mounted on a tripod at a fixed position near transect ten, facing out to sea. Camera angle was adjusted so as to include mainly birds flying in the over sea track of the wheel in each photograph. Trial runs indicated that this adjustment could be made by aligning the island of Boreray, which appeared in the background of photographs, in a standard position in the viewfinder relative to the central focussing circle. Most of the vertical extent, but not all of the horizontal extent of this outer wheel section was included in each photograph. Photographic coverage of the wheel is illustrated schematically in Fig. 3.33.

Photographs were taken with a 35mm lens (63° angle of view) on Ektachrome 200 slide film, rated at 400 ASA. Single Puffins in the outer wheel track took on average three

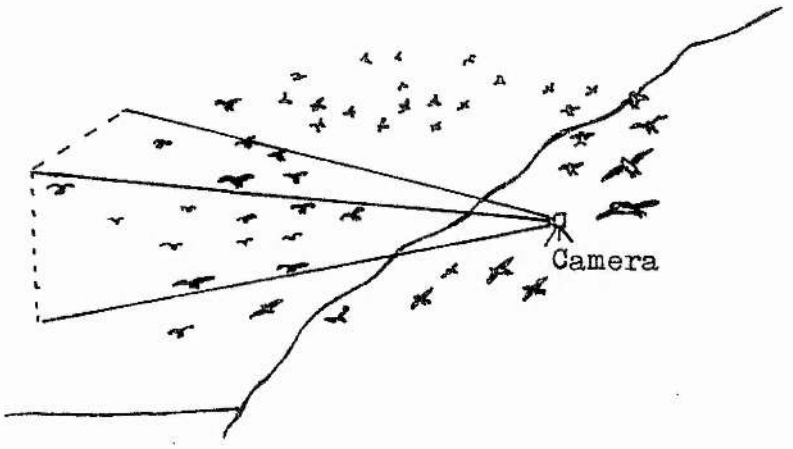


Fig. 3.33 Schematic illustration of photographic coverage of wheel

seconds to cross the field of view of the camera. Photographs were taken at three second intervals in sequences spanning at least 21 seconds, the mean time taken by a sample of 119 Puffins to fly an entire circuit of the wheel being 20.3 ± 5.8 seconds. Sequence number was coded directly on the film using a data back on the camera, and the shutter was triggered by an electric switch to avoid camera shake. All photographs were taken in winds less than Beaufort Force 4.

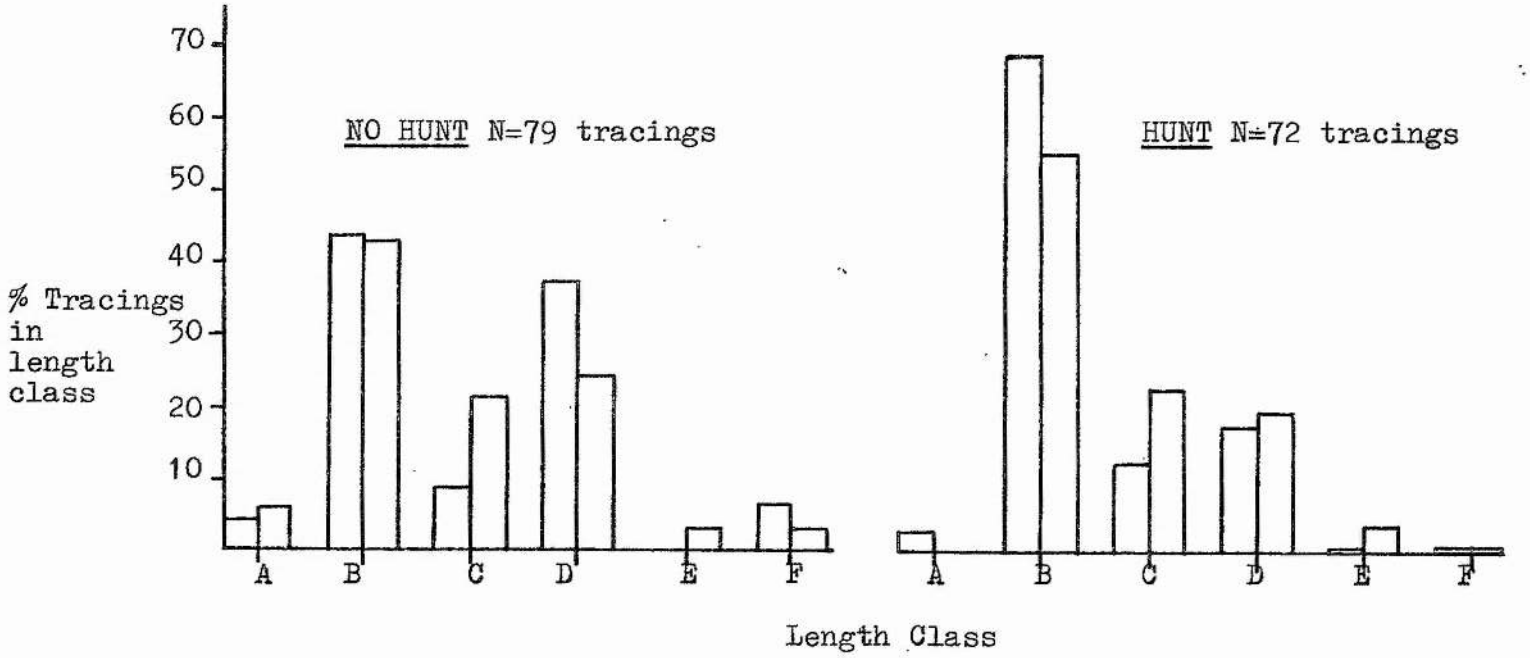
Slides were projected in an enlarger at x 9 magnification, again using the outline of Boreray for standard alignment. The outlines of projected Puffins were traced in ink on white paper placed on the enlarger baseboard. Puffins flying in the inner wheel track in the foreground of photographs were not traced. Most Puffins in the wheel flew in a relatively narrow band on the horizontal plane, and field observations indicated that photographs did register flying Puffins across the entire wheel breadth.

Three hunt and three no-hunt sequences were used in the main analysis. Calculation of the precise three-dimensional position of Puffins in the study wheel would have required either stereo-paired photographs, or sophisticated sensitometry of normal photographs outwith the scope of the present study. In order to obtain at least some three-dimensional information from photograph tracings, and as a precursor to analysis of spacing patterns, traced Puffins were assigned (PTO)

to one of two projected body length classes - less than or equal to 0.5mm and greater than 0.5mm.

This procedure was equivalent to vertically sectioning the wheel and reducing the three-dimensional scatter across the wheel of Puffins on either side of the section to two two-dimensional planes. An example of the scatter of tracing lengths from two hunt and two no-hunt photographs, measured to the nearest 0.25mm, is shown in Fig. 3.34. These measurements were made by placing a clear perspex ruler, marked out in divisions of 0.5mm, over tracings. (A judgement of a tracing length as being 'less than 0.25mm' was the lower limit of my accuracy in measurement.) In practice, very few tracings fell within the lowest length class, as illustrated in Fig. 3.34. This figure also illustrates the tendency for Puffins in the outer wheel track to be concentrated in a narrow range of size classes from $>$0.25mm to $\leq$1.0mm. This reflects the narrow range of distances between flying Puffins and the camera, and hence the concentration of Puffins in a narrow air corridor on the outer wheel track. (Puffins flying near the camera on the inner wheel track had a projected length of around 1cm.) The air corridor containing this outer wheel concentration was judged in the field to be less than 20 metres broad on the horizontal. Assigning Puffin tracings to the two length classes described here was thus, in most cases, equivalent to compressing the three-dimensional scatter of Puffins within corridors less than ten metres across to patterns of points on two two-dimensional planes, as illustrated in Fig. 3.35.

Nearest-neighbour distances between 1815 flying Puffins traced from 227 frames were measured using calipers.



Key: A 0.25mm, B>0.25-≤0.50mm, C>0.50-≤0.75mm, D>0.75-≤1.0mm, E>1.0-≤1.25mm, F>1.25mm

Fig. 3.34 Length of Puffins traced from hunt and no-hunt photographs

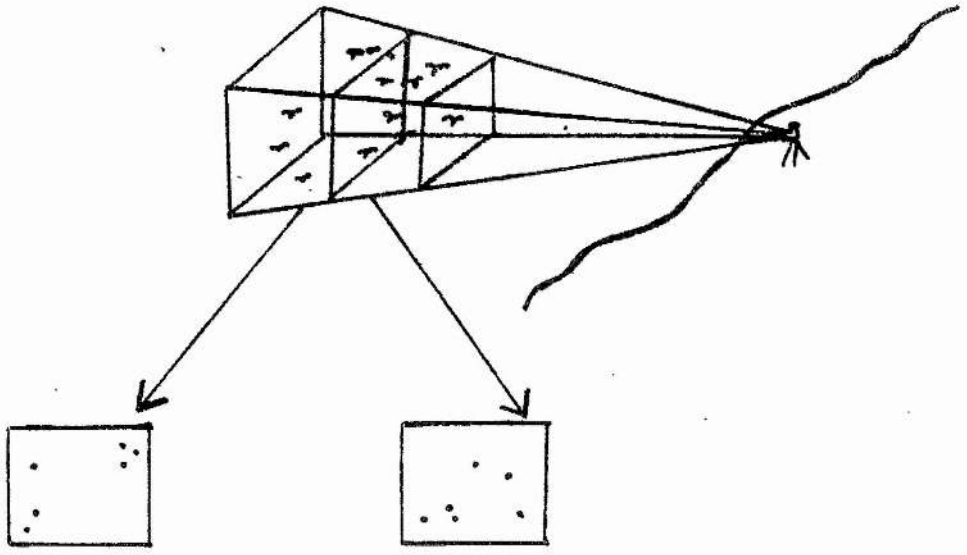


Fig. 3.35 Conversion of 3-d scatter of Puffins in wheel to two 2-d point patterns for spatial analysis

Measurements were made from the middle of the body of each Puffin to the middle of the body of the nearest Puffin in the same body length class. The nearest-neighbour statistic R_N, (Clark and Evans 1955) was calculated from measured inter-bird distances. This statistic gives a more powerful description of a point pettern than a simple calculation of mean point to point distance. It indicates both the direction and magnitude of a pattern's deviation, if any, from randomness. The statistic has a scale of values from zero to 2.149, random patterns having $R_N = 1$. Values less than 1 indicate aggregated patterns and increasingly smaller R_N values indicate increasing aggregation. Both mean point to point distance and the area within which points are contained are used to generate an R_N value for a pattern. Assuming that there was no difference in the average distance from the camera to Puffins within one length class photographed in hunt and no-hunt conditions, the effect of reducing the three-dimensional scatter of such Puffins to a two-dimensional point pattern would be similar for both conditions. As a result of standard X 9 projection of hunt and no-hunt transparencies, the area within which Puffins of one size class were contained would also be similar. On this basis, it would be valid to use the nearest-neighbour statistic as a measure of the relative, rather than absolute, scatter of Puffins wheeling in hunt and no-hunt conditions.

The assumption that within traced length classes, the average distance between flying Puffins and the camera was the same in both conditions was examined by measuring a sample of 400 tracings to the nearest 0.25mm. This sample comprised 100 tracings in each body length class used in the

main analysis from both hunt and no-hunt conditions. The proportion of birds assigned to each length class in both conditions was also compared for a sample of 226 tracings from ten hunt and ten no-hunt frames.

Results

There was no significant difference in the mean length of tracings within either length class between hunt and no-hunt conditions (t - test: $P > 0.4$), or in the proportion of birds assigned to either size class between conditions (χ^2 $P > 0.1$).

Inter-bird spacing decreased with increasing numbers of birds in a frame in both conditions (Table 3.20), the difference in spacing between frames with less than or equal to ten and greater than ten birds being significant in both conditions (+ hunt = Mann - Whitney U = 1892, $P < 0.00005$, N = 837 birds; - hunt: U = 2182.5, $P < 0.00005$, N = 978 birds). Puffins in frames with less than six and more than ten Puffins in total flew significantly closer together in hunt periods than did Puffins in frames with similar numbers in no-hunt periods. In both conditions, wheeling Puffins did not usually fly in one group, but were scattered across the photographed air space as illustrated by examples from hunt and no-hunt frames in Fig. 3.36.

With increasing numbers of birds per frame, R_N values decreased to below 1 in both conditions, indicating that the more Puffins there were in a standard air space, the more aggregated was their dispersion pattern (Fig. 3.37).

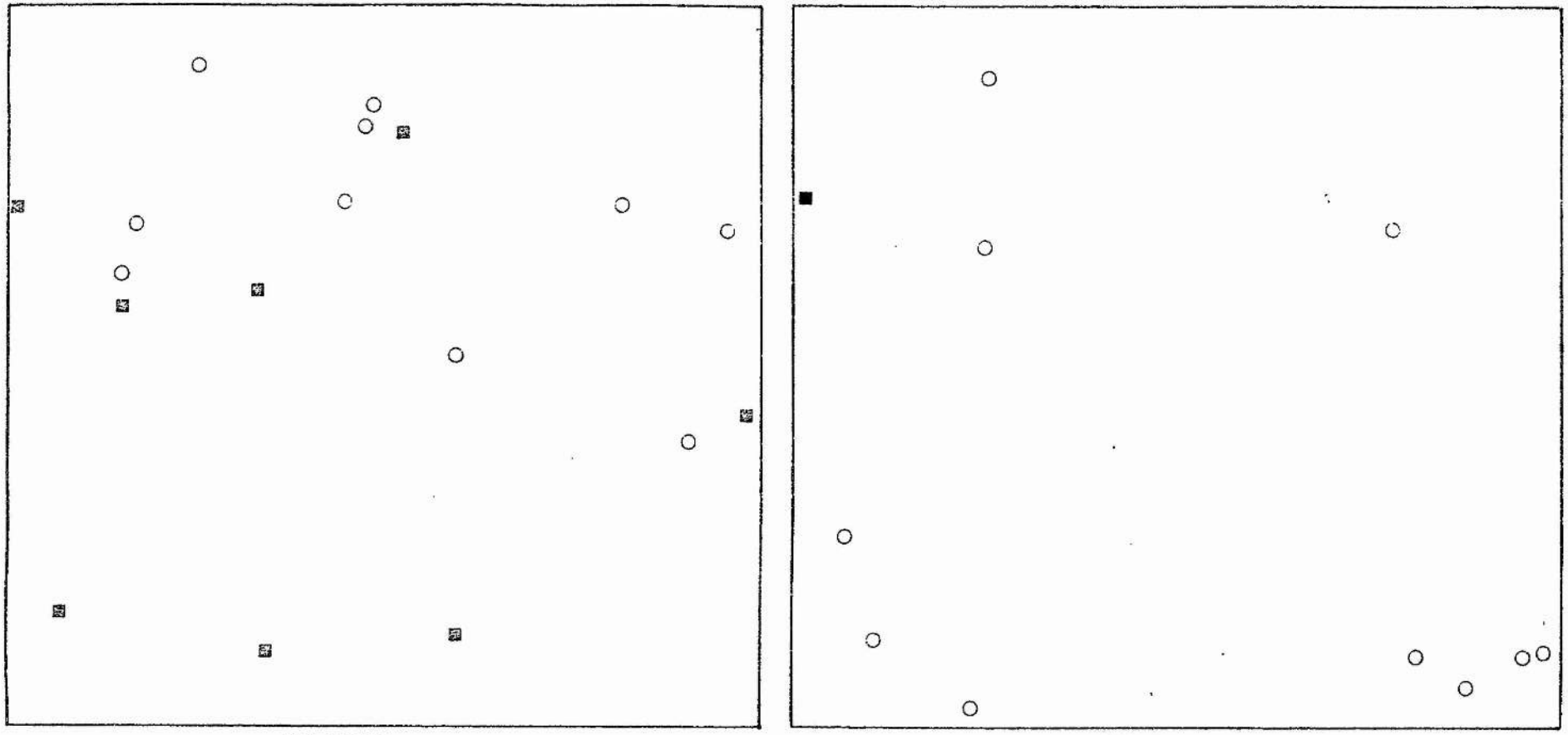


Fig. 3.36 Spatial distribution of Puffins in the same wheel during parts of no-hunt and hunt photograph sequences

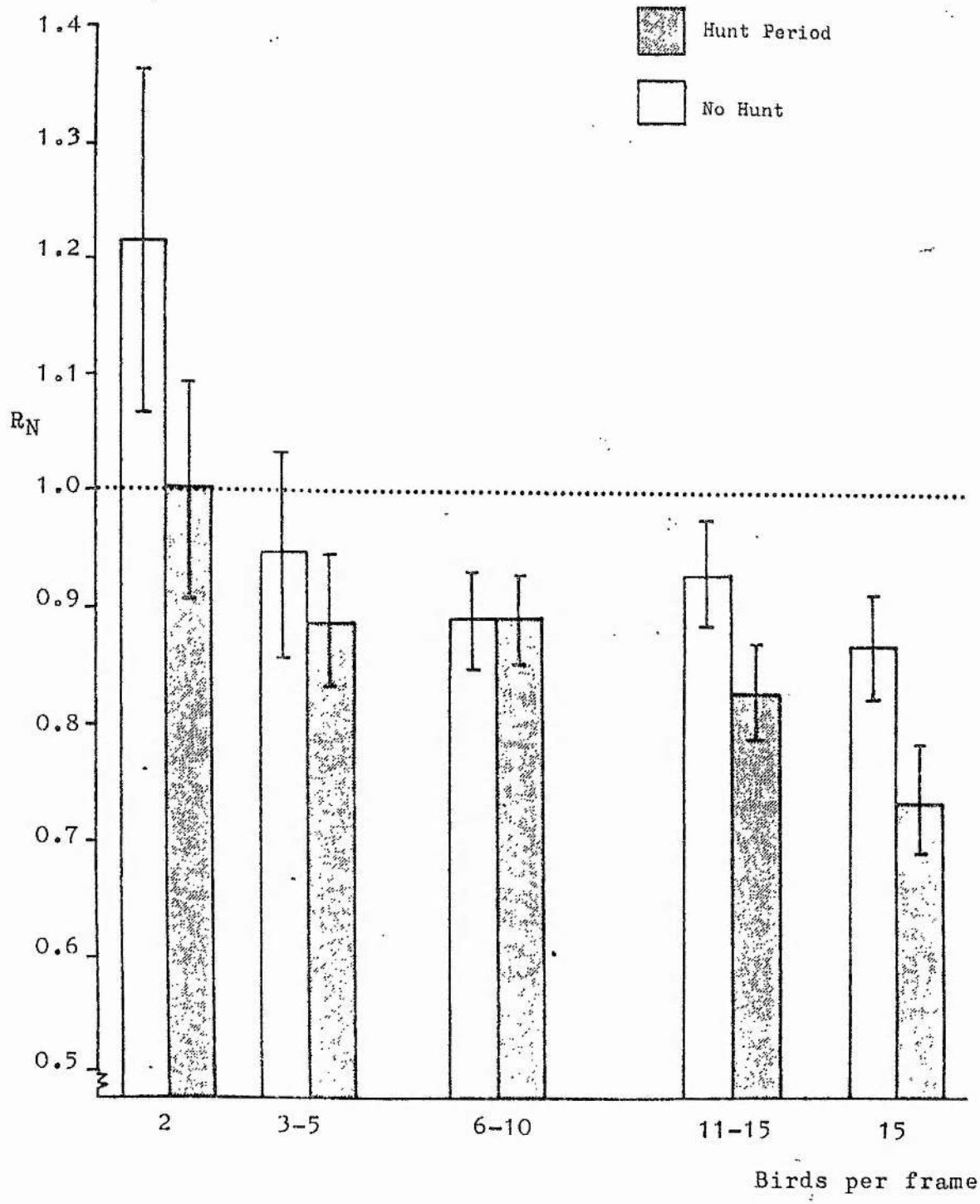


Fig. 3.37 Dispersion of Puffins in a wheel (R_N) with and without a hunting gull in the vicinity

Table 3.20 Real spacing (bird lengths) ± hunt conditions of wheeling Puffins

Birds per Frame	Spacing + Hunt	Spacing - Hunt	Mann - Whitney U Prob.
2 - 5	50.0 ± 27.1	56.8 ± 32.4	0.0001
6 - 10	32.2 ± 11.4	31.7 ± 12.7	NS
> 10	23.6 ± 5.5	26.0 ± 7.5	0.0001
Overall	37.7 ± 21.7	37.0 ± 23.5	NS
N	116 Frames	111 Frames	

The difference in R_N values between frames with less than or equal to ten and greater than ten birds was significant only in hunt sequences (+ hunt: $U = 1403$, $P = 0.038$, $N = 837$ birds; - hunt: $U = 1434.5$, $P = 0.35$, $N = 978$ birds). In hunt sequences birds were also significantly more clustered than in non-hunt sequences when more than ten birds were recorded per frame ($U = 660$, $P = 0.0256$, $N = 953$ birds).

If individuals in a population dispersed over a plane form pairs at random in which each member is the nearest neighbour of the other member of the pair ('reciprocal nearest neighbours' (Clark and Evans 1955)) it can be expected that such reciprocal nearest neighbours will comprise 0.6215 of the population (Pielou 1969). There was no difference between this expected random proportion and the observed proportion of birds falling in such pairs for either hunt or no-hunt conditions (Overall mean = 0.640 ± 0.01, $\chi^2 = 1.78$, 2-t, $P > 0.1$, $N = 1750$ birds). Thus, in any period, as the number

of Puffins in a given air space increased, the distance between Puffins decreased. When a hunting gull was in the vicinity, the distribution of wheeling Puffins was significantly more clustered than at other times, this clustering increasing as the number of birds in the air space increased. This increased clustering in hunt periods was likely to be due to the formation of groups of more than two birds.

Discussion

The analyses presented here were based on a simplification of photographic data, with the three-dimensional scatter of flying Puffins being reduced to two-dimensional patterns of points. Results from fine scale measurement of traced Puffins support the assumption that within traced length classes the average distance between flying Puffins and the camera was the same in both hunt and no-hunt conditions. The effect of simplifying spatial data was thus similar in both conditions, vindicating the use of the nearest neighbour statistic as a measure of the relative dispersion of wheeling Puffins in hunt and no-hunt periods.

The suggestion that Puffins in a wheel tended to fly closer together in hunt periods than at other times, made earlier on the basis of data on looping behaviour, is supported by data on inter-bird spacing. Spacing data also indicates that clustering in response to a hunting gull was more pronounced the more Puffins there were flying in a standard air space.

Gulls caught Puffins most easily when there were few birds in a wheel. Photographic data indicates that gull performance may have been influenced by the relatively large

inter-Puffin distances and the lack of bunching of Puffins in such wheels. Similarly, this data indicates how Puffins in Sparse area wheels might be particularly vulnerable to gull attack. Even if birds in a Sparse area wheel responded to a hunting gull by making more frequent loops during wheel circuits, this behaviour would not necessarily lead to bunching.

Synchronisation of movements to, from and within the colony with many other Puffins could thus increase an individual bird's chances of joining a bunch of other Puffins when an aerial predator is hunting and potentially reduce its chances of being caught. When there were few Puffins in a wheel, the birds' anti-predator behaviour did not inevitably lead to bunching. A gull hunting in the vicinity of a wheel with few Puffins thus had access to isolated prey, this being a possible reason why gulls concentrated hunt effort in times when relatively low numbers of Puffins were wheeling.

3.6 DIFFERENCES IN WHEELING BEHAVIOUR BETWEEN COLONIES

Differences in the duration and location of wheels or similar flight behaviour at different colonies are compared qualitatively here to indicate how these may be influenced by colony habitat, colony size and the presence of other species. These comparisons also illustrate further how wheeling may allow individual Puffins to group with other Puffins.

Wheels on the Isle of May were associated with periods when many Puffins were arriving at or leaving a colony area

and with scare periods (cf Nettleship 1972). This was also the case for small boulder breeding sites on Grimsey Kirk Beach, and for the Sparse Puffin area on Dun.

By contrast, wheels over the Dense Puffin areas on Dun were an almost perpetual feature of the colony during daylight hours (cf Harris 1980). This was also the case on Mykines.

At the Vik east cliff, the only wheeling activity noted after mid-morning during five days' observations was after 21.00 hours. Most Puffins flying near the cliff before dusk were either fish carriers or birds about to fly out to fishing grounds. Fish carriers flying near the cliff tended to make erratic looping circuits before landing, often with more than one loop in a single circuit.

During most of the day at Vik, circling flight behaviour performed by groups of birds, reminiscent of wheeling but less regular in air track, took place not at the colony itself, but over the beach and shoreline, 0.5 to one kilometre from the breeding cliff. Some groups of Puffins flying in this way were joined by other groups or singles before flying out to sea and before flying in to the colony.

At Herjólfur's Valley cliffs on Heimaey, another inland Icelandic colony similar in burrow habitat to Vik, wheeling activity followed the same pattern as the Isle of May.

Inter-colony differences are summarised in Table 3.21. These comparisons suggest that the extent of wheeling throughout the day is in part a function of colony size. Large high burrow density colonies have more birds arriving at or leaving a given area throughout the day than smaller colonies.

Table 3.21 Wheel duration and Puffin colony characteristics

Colony	Situation	Breeding sites	K-parasites	Aerial predators	Ravens Gleaning	Wheel duration	Wheel-like behaviour out from colony
Isle of May	Island Slopes	6,000+	+	-	-	Occupation/ desertion/ scare periods	-
Dun Sparse	"	5,000+	+	L.marinus	-	As Isle of May	-
Dun Dense	"	20,000+	+	L.marinus	-	All day	-
Mykines, Village area	"	c60,000	+	-	-	As Dun Dense	-
Grimsey - Kirk Beach	Boulder Beach	< 500	+	L.marinus	-	As Isle of May	-
Vik, East Cliff	Inland Cliff	< 10,000	+	L.marinus	+	Dawn and evening	+
Herjólf's Valley	"	5,000+	+	?	-	As Isle of May	-

Vik is the only colony visited where wheeling was not seen during most of the day at the colony itself. Comparison with the Herjólfur's Valley colony suggests that this may have been due to the high frequency of kleptoparasitic attacks on Vik Puffins, combined with, but not solely due to, the inland colony site.

Aerial activity out from Vik also indicates how wheeling, as suggested previously, may allow individual Puffins to group with other Puffins flying to and from the colony. In the absence of wheels near the colony, Vik Puffins made looping flights away from the colony. This behaviour was associated with aerial grouping and was not observed at other sites where wheeling occurred throughout the day over the colony itself.

3.7 OTHER ASPECTS OF AERIAL GROUPING BY PUFFINS

a) Synchronisation of flights to roost by small groups of Puffins

Around sunset, there was an increase in the number of birds moth-flying (see Appendix) over the colony. In moth-flight, a Puffin arched its body and kept the wings held up above its back, propulsion being by rapid fluttering of the outer wing feathers rather than by deep wing beats. Moth-flight reduced a Puffin's airspeed to about half that of normal flight. It was used infrequently throughout the day, but was most noticeable around dusk, when pairs of birds, using moth-flight, left the colony together.

Puffins in such pairs flew very close together, side by side. (Occasionally, Puffins in a moth-pair flew so close

that their wing tips touched and the birds veered away from each other.) The mean onset of paired moth-flying in evenings between 8 and 19 May 1978 on the Isle of May was 19 minutes after sunset (± 2.04 minutes, N = 4 evenings).

Moth fliers in pairs headed out to sea without re-joining a colony wheel significantly more often than singleton moth fliers on the Isle of May (Table 3.22) and Mykines (Mykines: Fisher exact p = 0.00013, N = 21 birds). 42.11% of Isle of May moth pairs which did not re-join a wheel landed in small water groups 0.5 Km or more out from the island (N = 19 pairs). The rest did not land within binocular range. Colour marked birds from known breeding pairs were seen leaving Colm and Little Hole study areas on the Isle of May together using paired moth flight. Some single moth fliers were joined by another Puffin above the colony, or themselves joined a moth pair, the birds then moth flying together out to sea.

Table 3.22 Dispersal of single and paired moth fliers from Colm area, Isle of May, 8/5 to 19/5/78

	Re-join wheel or land at colony	Fly out to sea	
Single	12	2	14
Pair	7	19	26
	19	21	40

Pairs of moth fliers fly out to sea more than single moth fliers - Fisher exact p = 0.00049.

Moth flying was thus associated with the synchronised departure of pairs and small groups of Puffins flying out from a colony to roost. Differences in the dispersal behaviour of single and paired moth fliers indicate that this behaviour was an attempt by individual Puffins to leave the colony with at least one other Puffin.

Moth flying is also used away from colonies. M. Tasker (pers. comm.) has observed Puffins which have been fishing moth flying over flocks of Puffins at feeding grounds in the North Sea before flying away from the feeding flocks. In this context, moth flight might help Puffins group at fishing grounds before flying to a colony.

b) Grouping of Puffins flying to and from fishing grounds

Since Puffins flying in with fish to a breeding colony can be attacked by kleptoparasites as well as predators, fish carriers might be expected to group with other Puffins both at and away from the breeding colony. This section addresses the question whether Puffins do group with other Puffins on fishing trips, and if so, where this grouping takes place.

Methods

Much of the data to follow was obtained at the East Cliff Puffin colony at Vik in Iceland. This colony is a particularly good site for observing the traffic of Puffins to and from fishing grounds. Since the colony is about one kilometre inland, observations can be made of Puffins flying overhead at greater distances out from the colony than is normally feasible at other sites. Puffins at this colony are also subject to an unusually high frequency of klepto-

parasitic attacks, principally by Arctic Skuas (cf Arnason and Grant 1978).

Observations of the pre- and post-fish delivery behaviour of Vik Puffins were made from concealed vantage points near burrows at the top of the East Cliff and from an open position at the base of the cliff at least 100 metres away from watched delivery burrows. Focal animal sampling was used, a Puffin seen flying near the cliff with fish usually being watched from the time it was first sighted until it delivered its fish, emerged from a burrow within five minutes post delivery and flew out to sea again to the limit of binocular range. Monitoring of some fish carriers ended with the subject being chased out of sight by kleptoparasites. Other observations of Vik fish carriers and of Puffins flying out to sea were made both at the cliff base and at two sites on the beach, one about half a kilometre from the cliff, the other near the shoreline about a kilometre from the cliff. At these sites, the number of Puffins flying overhead was scored for 10 second time intervals during a watch, the traffic of outgoing flyers being scored in different watches from the traffic of incoming flyers.

On St Kilda, observations of fish carrying Puffins flying in towards Dun were made by cassette record of the number of Puffins crossing the foreground of a 10 x 50 binocular field of view centred on the mid point of the mouth of Village Bay, from a vantage point at Oiseval on Hirta. Observations of birds joining rafts of Puffins off the Isle of May in the pre-laying period were made by a similar method from a vantage on the Island Rocks.

The flight orientation and grouping behaviour of Puffins leaving breeding sites at Grimsey Kirk Beach was scored around dawn on one morning. The number of Puffins flying across the bows of a ship sailing near feeding grounds was scored for half minute periods of a 50 minute watch made during a voyage from Heimaey, Westmann Islands, to Thorlakshöfn in southern Iceland.

Other observations presented here were collected casually and are condensed from field notes made during visits to colonies for purposes other than watching Puffins flying to and from fishing grounds.

Results

Puffins which roosted ashore began to fly out to fishing grounds around dawn. These departures tended to be clumped in time as illustrated by data from the Isle of May (Fig. 3.38).

Individual birds did not always fly out to sea immediately after emerging from a burrow. On the Isle of May, Puffins often came out of a burrow around dawn, looked around and went back down the burrow again. They might then re-emerge a few minutes later and fly out to sea. On St. Kilda, I noticed several hundred Puffins standing outside burrows on the Dense summit slope early in the morning on some days before flying out to sea. After taking off, a Puffin might fly in a wheeling circuit over the colony area around its burrow and land again before finally heading out to sea. On Grimsey, for example, the first four Puffins leaving the Kirk Beach breeding sites after dawn on 4 August 1979 made an average four circuits of the bay before heading out to sea.

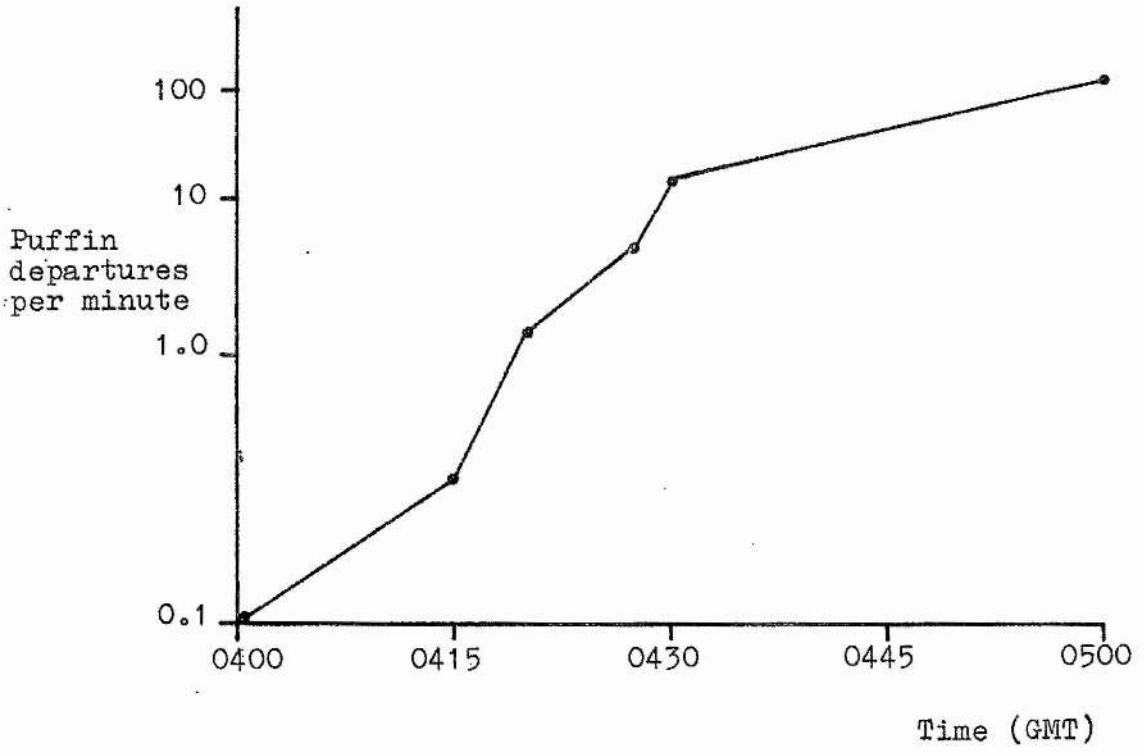


Fig. 3.38 Rate of first early morning Puffin departures from Burrian, Isle of May, 21/5/75

Although there was thus sometimes considerable synchronisation of early morning departures from a colony, not all Puffins from a colony area flew out to sea in the same direction. This is illustrated by data on the over sea flight orientation of 28 birds observed flying out from the Grimsey boulder beach colony between 05.00 and 06.00 on 4 August 1979 (Fig. 3.39). On Grimsey it was also noticed that some birds in groups of flying Puffins which had formed near the colony split away from the group a few hundred metres offshore and flew in a different direction from the rest of the group.

The majority of departures from the colony later in the day were not synchronised with departures of other Puffins at the colony itself. For example, birds departed at random from Vik during a 75 minute period between 16.45 and 18.00 hours on 16 August 1979 (Fig. 3.40), as judged by the fit of the observed departures to an expected Poisson distribution using 10, 20, 30 and 40 second time windows (all 2 - tχ^2 probalities > 0.1).

Grouping did occur out from the colony. This is illustrated by data on the mean and range of Puffin groups observed flying out to sea over observation points at different distances from the Vik cliff, group size increasing as distance from the colony increased. (Fig. 3.41). Significantly more Puffins flying out over the shore at Vik were in groups of two or more than were Puffins flying out in the same direction farther inland ($\chi^2 = 16.15$, $p < 0.0005$, 2 df, N = 344 birds). Some groups and single Puffins flying out across the Vik beach were seen circling before heading out to sea. Qualitative field notes indicate that this was

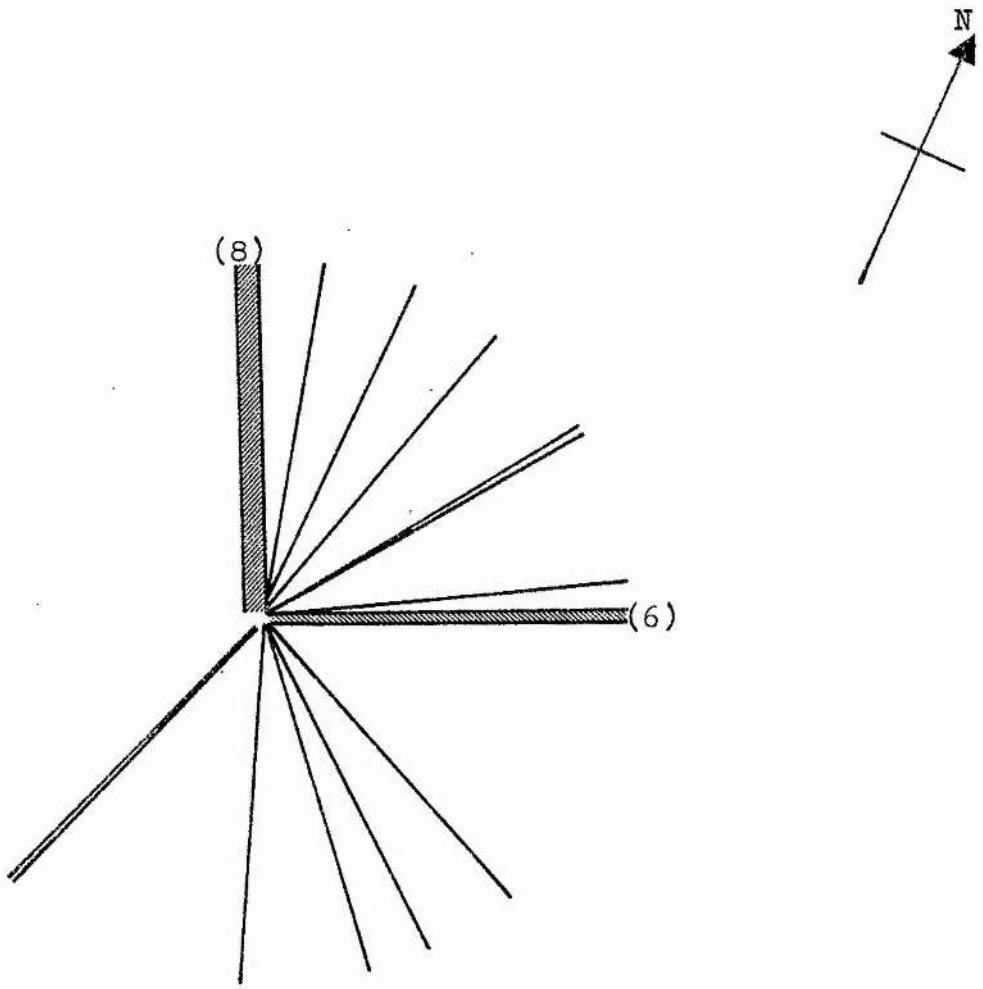


Fig. 3.39 Flight directions of first early morning Puffin departures from a Grimsey colony

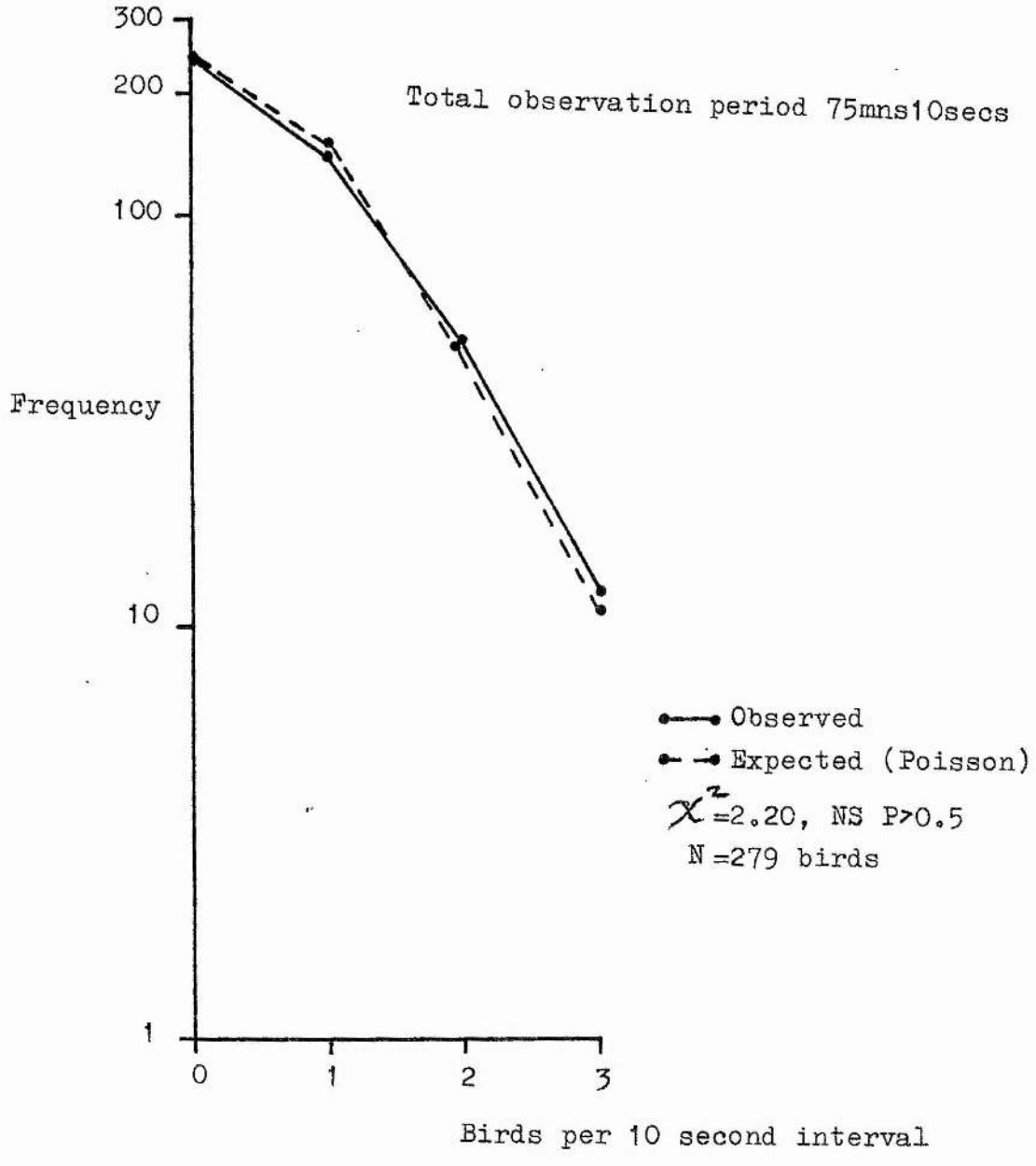


Fig. 3.40 Number of Puffins observed departing from Vik East Cliff colony per 10 second interval and number expected if departure timing random (Poisson distribution)

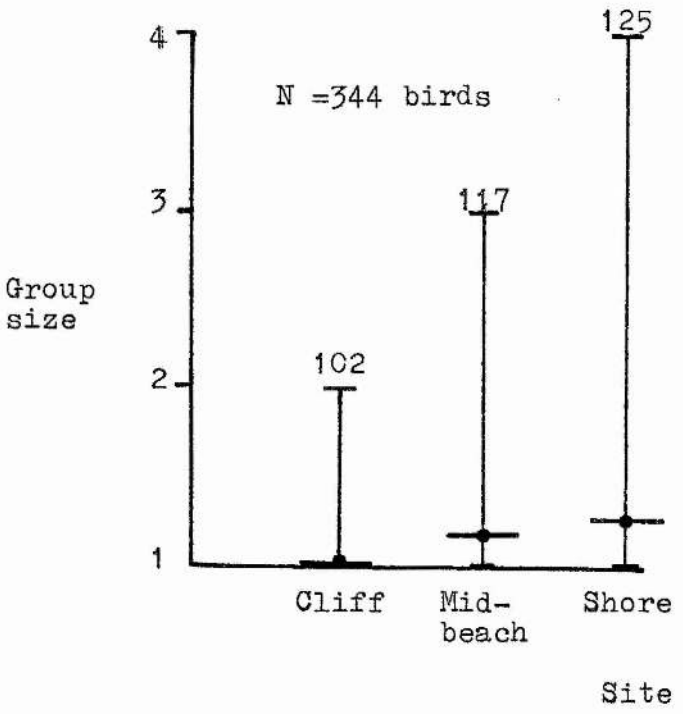


Fig. 3.41 Mean and range of Puffin group sizes on outward flights from Vik East Cliff

associated with the formation of larger groups.

At sea, Puffins tend to be distributed in small groups on the water (cf. Ashcroft 1976, Taylor 1978). Puffins flying over a fishing area also tend to fly near other Puffins. This is illustrated by data on the number of Puffins seen flying across the bows of a ship sailing near an auk fishing area off southern Iceland, when 92% of Puffins seen were flying in the same half minute time period as at least one other Puffin (Table 3.23).

Table 3.23 Time interval between Puffins flying across an Icelandic sea area

Time (mns) between successive Puffins	Observed	Expected (Poisson)	χ^2
< 0.5	79	36.39	49.89
0.5- 1.	2	31.30	27.43
≥ 1	5	18.31	9.68
	86	86	87.0 $P < 0.0001$, 1df

Puffins tended to fly back to a colony from the fishing grounds in groups. At a large colony, such as Mykines, groups could comprise more than twenty birds and the incoming traffic of fish carriers at peak feeding times could be immense. For example, the mean size of 50 groups observed flying in to Mykines across a 10 x 50 binocular field around 18.30 hours on 23 July 1979 was 9.34 ($\pm$ 0.43, N = 467 birds). At this time it was estimated that in excess of 12,000 fish carriers per hour were flying in to Mykines from the north west.

Arrivals of Puffins flying in to the Isle of May and St Kilda were not distributed randomly in time (Table 3.24). In each case, deviation from random was mainly due to there being more time windows with no birds recorded than would be expected if arrivals were temporally random. Data on fish carrier arrivals at St. Kilda also illustrates how more large groups were recorded than would be expected at random (Fig. 3.42).

Puffins did not fly in to the colony at a constant rate. A minute when less than 30 Puffins were observed could be followed by a minute when more than sixty were seen (Fig. 3.42). Fluctuations in return rate appeared to have some regularity, but investigation of whether returns to the colony are truly cyclic would require sophisticated time-series analysis outwith the scope or aims of the present study. Moth flying at the fishing grounds, as has been described earlier, could facilitate the formation of such large groups at feeding areas before Puffins fly back to a colony.

Groups flying in to the colony tended to fragment before reaching the land. This was noticed at St Kilda, Mykines and Vik. The fragmentation of large groups off Mykines was spectacularly obvious, since many birds tended to veer away from a group simultaneously to different parts of the colony, giving group break up the appearance of an exploding bombshell. Data on the mean size of groups flying in to Vik above observation points at different distances from the colony illustrates this fragmentation, maximum observed group size decreasing from 18 at the shore to three at the

Table 3.24 Non random timing of Puffin returns to colony from sea

Area	Date	Observation period (mns)	Time window (secs)	Birds	$\bar{x}$ Group per window	χ^2	df	p random 2-t
	10.4.77	10.33	5	157	1.27	17.53	2	<0.001
Isle of May	10.4.77	-"-	10	-"-	2.53	6.11	2	<0.05
Village Bay	19.7.77	31	10	1175	6.32	239.61	8	<0.001
Village Bay	19.7.78	17	10	271	2.66	334.39	5	<0.001
Village Bay	19.7.78	42.5	10	2016	7.87	361.79	2	<0.001

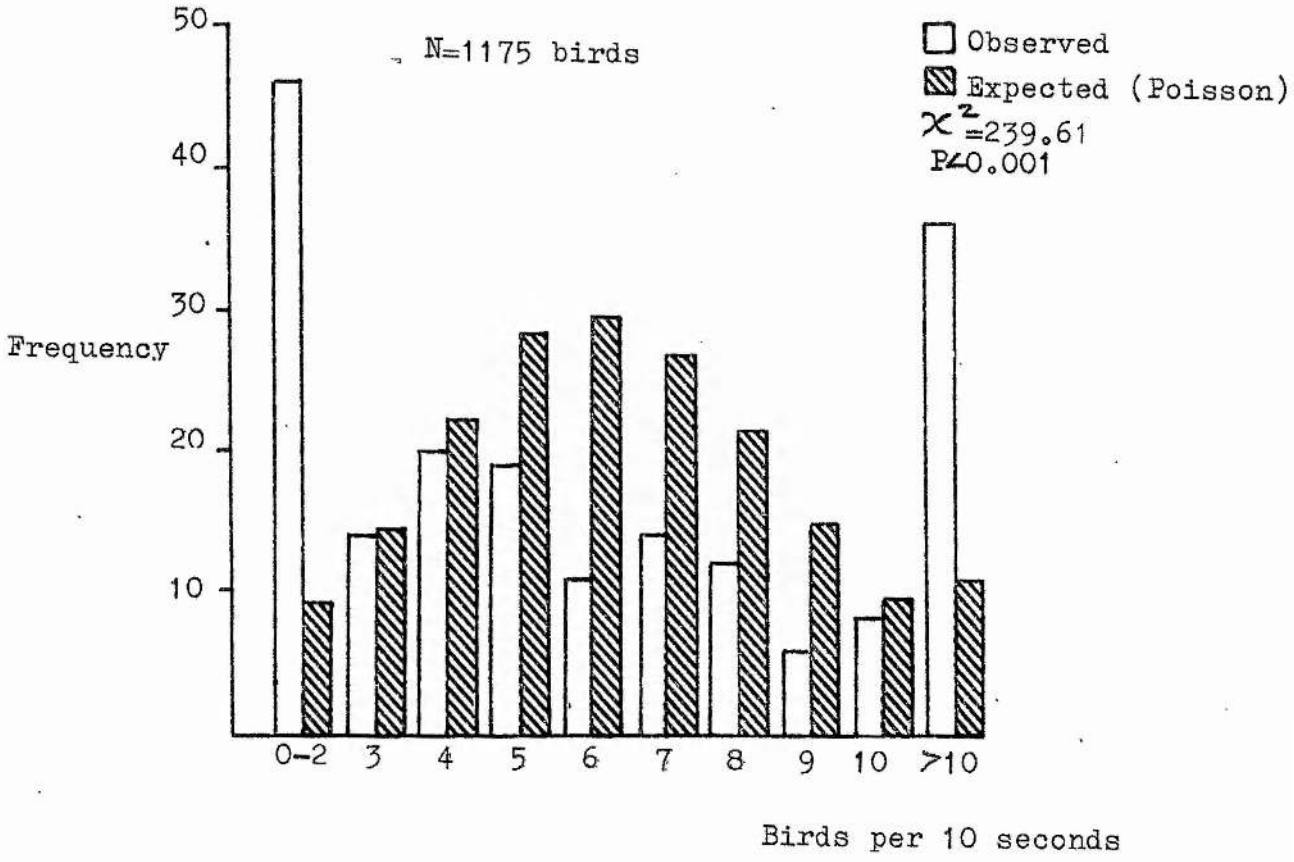


Fig. 3.42 Fish carrier arrivals at Village Bay in ten second periods in 31 minutes observation 19/7/77

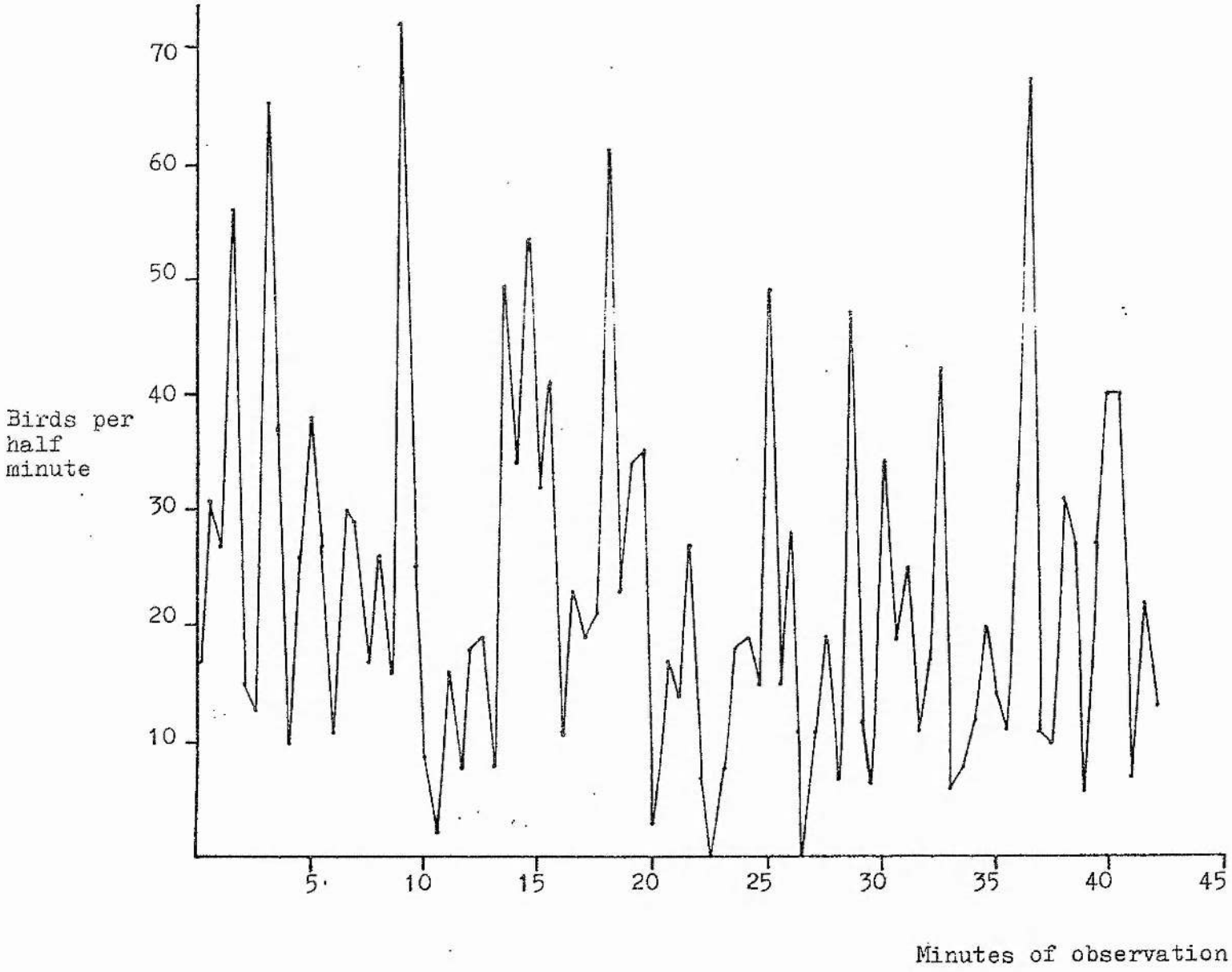


Fig. 3.43 Fluctuations in number of Puffins returning from fishing grounds to Village Bay during 42 minutes observation, 19/7/77

breeding cliff (Fig. 3.44). Significantly more incoming flyers were seen in groups of two or more at the Vik shore than nearer the colony (χ^2 = 97.0, $P < 0.0005$ 1 - t, 1 - df, N = 642 birds). A significantly greater proportion of singletons were recorded on outward flights than on inward flights at Vik (χ^2 = 218.58, $P < 0.0005$, 1-t, 1-df, N = 986 birds).

Puffins flying in to the Vik beach often circled between half and one kilometre out from the cliff, as described earlier for outward flyers. This behaviour was associated with grouping. Although groups which formed near the beach usually fragmented while flying in to the cliff, the limited data available indicate that wheel-like circling behaviour out from the cliff may have increased an individual Puffin's chances of flying in to its own burrow area with another Puffin (Table 3.25).

Table 3.25 Merger and fragmentation of fish carrier groups flying in to Vik East Cliff colony

Group size at beach	Circle beach	Join another group	Split near cliff
2	-	-	1,1
2	-	-	1,1
2	-	-	1,1
2	-	-	1,1
2	-	-	1,1
2	-	-	1,1
2	-	-	-
4	+	+5	3,2,2,1,1
5	+	+7	4,3,2,2,1

Once at the colony, fish carriers might join a wheel and it has already been shown that such birds tended to make fewer

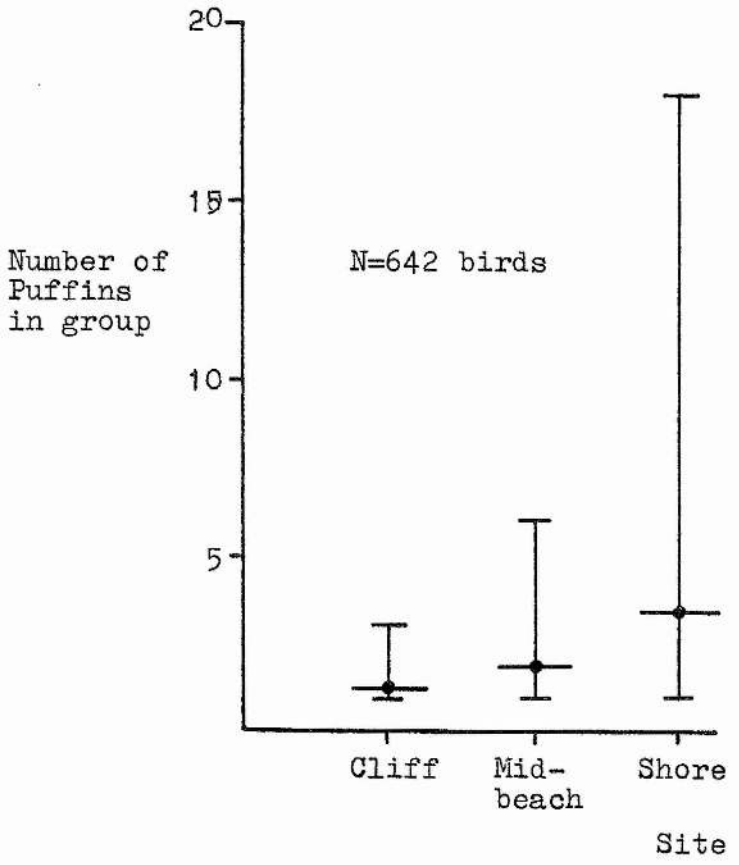


Fig. 3.44 Mean and range of Puffin group sizes on inward flights to Vik East Cliff

wheel circuits before landing than Puffins without fish.

At Vik, most Puffins flying near the East Cliff before dusk were either fish carriers or birds about to fly out to fish. The mean number of flight circuits made before landing by Vik fish carriers was 2.68 ($\pm$ 0.47, N = 77 birds). Three fish carriers, not harassed by kleptoparasites, turned back out from the cliff and flew towards the shore after two, four and seven circuits respectively.

At many colonies where Puffins are subject to kleptoparasitism by gulls, but not skuas, most fish carriers run down a burrow immediately after landing. (For example, different observers on the Isle of May and Dun have commented that this behaviour makes monitoring fish delivery frequency difficult.) At Vik, 28.9% of fish carriers delayed going down a burrow after landing for periods ranging from three to 16 seconds ($\bar{x}$ = 2.2 $\pm$ 0.81 seconds, N = 45 birds). Mean delivery time for birds which emerged within five minutes of going down a burrow was 44.7 seconds ($\pm$ 5.9 seconds, N = 27 birds). Birds which delayed pre-delivery, or which landed within five seconds of a Puffin at a neighbouring burrow, had significantly shorter delivery times than other birds (Mean 31.1 $\pm$ 4.8 seconds, N = 10 delay birds; Mean 52.8 $\pm$ 8.4 seconds, N = 17 no delay birds; $t = 2.80$, $P < 0.01$).

After emerging, 70.6% of Vik Puffins did not take off immediately, but stood at the burrow entrance for between two and 95 seconds before flying out to sea ($\bar{x}$ = 16.1 $\pm$ 3.96 seconds, N = 34 birds). All birds known to have delayed before going down a burrow delayed after emerging, significantly different from birds which were known not to have delayed pre-delivery, 53% of which took off immediately

after emerging (Fisher exact $P < 0.0001$, N = 27 birds).

Pre-delivery delay duration was positively correlated with post-delivery delay duration ($r_s = 0.675$ (tie-corrected), $P < 0.001$, N = 27 birds) (Fig. 3.45).

Significantly more Puffins which delayed pre- or post-delivery were joined by a neighbouring Puffin on the ground than birds which did not delay (Fisher exact p = 0.015, N = 34 birds). Joining was mostly due to one or more landings at another burrow or burrows within one metre of the delaying bird (six out of eight cases). On two occasions a bird emerged from a burrow near the delaying Puffin.

25% of 24 Puffins which delayed post-delivery took off within two seconds of a neighbouring Puffin, significantly different from Puffins which did not delay post-delivery, none of which followed a neighbour out to sea (Fisher exact p = 0.049, N = 34 birds).

To summarise - Except around dawn, the departure of Puffins flying out to fishing grounds from a colony was for the majority of birds, not synchronised with the departure of neighbouring birds at the colony itself. Many Puffins did group with other Puffins out from the colony, this grouping beginning within one kilometre of the breeding site at Vik. Many fish carriers returning to the colony flew back in groups with other Puffins. At Vik, some groups merged with other groups out from the colony before continuing the inward flight. These groups fragmented near the colony. Fish carriers often participated in a wheel over the colony, or in the absence of other near flying Puffins made erratic circuits near their burrow. Except at Vik, most fish carriers ran down a burrow immediately after landing. Some

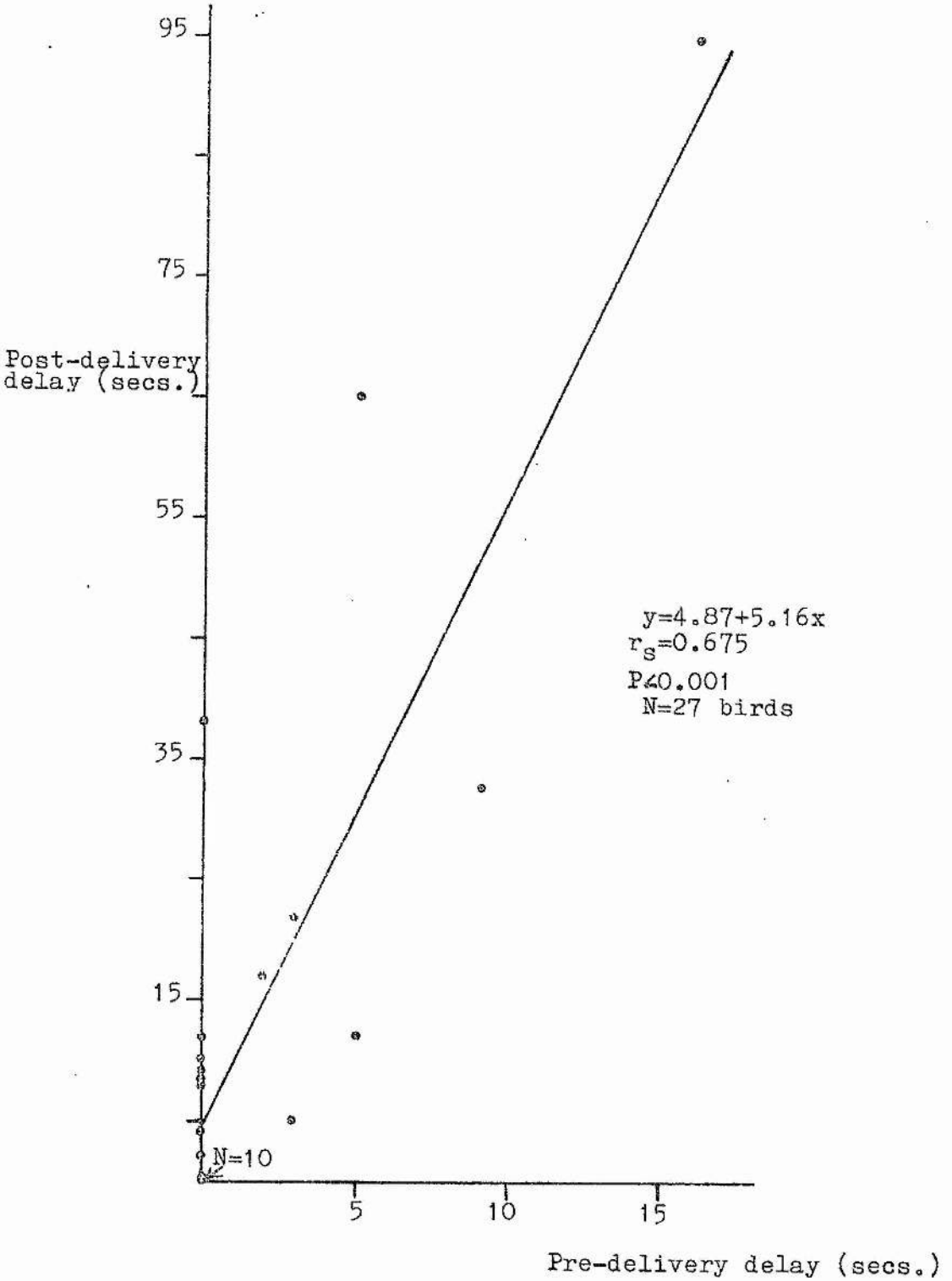


Fig. 3.45 Pre- and post-delivery delay times of fish carrying Puffins after landing at burrows in Vik East Cliff colony

fish carriers which delayed pre- or post-delivery at Vik were joined by other Puffins on the ground, and took off soon after another Puffin.

Discussion

Whereas Puffin departures from the Vik East Cliff were random (Grant 1971, this study), Ashcroft (1976) found that departures from a Skomer colony were not random in time. Ashcroft stated that unless Skomer Puffins joined a raft they flew straight out to sea from the colony without joining a wheel, but did not present data on this. Puffins in the Ainov Islands joined wheels both on arriving at a colony with fish and before moving to fishing grounds, the birds leaving the wheels in small groups to descend to feeding areas (Skokova 1962). Although there were no wheels or rafts at the inland Vik colony, Puffins performed wheel-like behaviour over the shore, this being associated with grouping of incoming and outgoing flyers. I suggest that differences in the phasing of departures from Vik and Skomer could be due to differences in wheeling and rafting location at the two colonies. Further field work at Vik, and at other colonies where wheels and rafts form near the colony, will be needed to investigate this suggestion.

Ashcroft (1976) showed that Puffins tend to group flying to, at, and flying from fishing grounds, and that landings of fish carriers at neighbouring burrows were clumped in time. Data presented here extends these findings and shows that groups which form at different stages of fishing trips are often transient - Fish carrying Puffins which land together at a colony have not necessarily left the colony

together or fished together. This has a bearing on the question of whether Puffin colonies have an 'information centre' function for birds breeding there, with individuals which have not found fish being able to follow other individuals which have already located fish to profitable feeding areas (cf. Ward and Zahavi 1973). Future investigation of the relevance of the information centre hypothesis to Puffin colonies should concentrate on the spatio-temporal patterning of departures from colony areas and wheels, not arrivals of fish carriers at burrows.

Observations at the Ainov Islands, and my data on the wheeling behaviour of individual Puffins, indicate that temporal clumping of fish deliveries to neighbouring burrows is likely to be due to fish carriers joining a wheel before landing. Since Puffins fly in a wheel track which passes over their own burrow, there is a chance that a fish carrier which joins another fish carrier flying in the same section of a wheel can land with the other Puffin. Vik Puffins attempt to group away from the breeding site in the absence of wheels at the colony and also make looped flights near their burrow on arriving at the colony, looping having already been described as a means by which a Puffin could attempt to group with other Puffins in the air.

Pre- and post-fish delivery delaying behaviour of Puffins at Vik increased the chance that a Puffin would be joined by a neighbouring Puffin on the ground. Puffins delaying post-delivery were also more likely to fly from the colony with a neighbouring Puffin. My observations at other colonies show that post-delivery delaying behaviour is widespread, whereas pre-delivery delays are unusual. Once again, this suggests

how wheeling could facilitate grouping of birds arriving and departing for the sea. Pre-delivery delays may be both unnecessary and costly at sites where Puffins can group in the air above the colony, e.g. Puffins delaying entry to burrows at Vik were sometimes attacked by kleptoparasitic gulls. Post-delivery delays do not risk food loss and could be used more widely by Puffins as a means of joining other Puffins on outward trips from the colony.

Grant (1971) described wheel-like behaviour over the Vik beach and shore as the 'turn-back phenomenon' and suggested that it may function to reduce the risk of kleptoparasitic attack. He interpreted this behaviour as an 'apparently straightforward avoidance of skuas at the shore and colony', suggesting that if a skua was patrolling near a Puffin's burrow, the Puffin delayed its flight in to the colony. I disagree with this interpretation for a number of reasons. Grant showed that the frequency of turn-back behaviour increased as Puffin arrival frequency decreased, although skua numbers were approximately constant throughout. If turn-back behaviour was 'straighforward' avoidance of skuas, its frequency per Puffin should vary as a function of skua numbers, not Puffin numbers.

My observations show that turn-back behaviour was assso-ciated with the formation of aerial groups, and that this grouping occurred both on flights in to and out from the colony. Puffins without fish on outward flights have no need to avoid a skua. Turn back behaviour thus appears to be an attempt to form aerial groups. This may be in part a response to kleptoparasites, but is not simple avoidance of skuas.

These, and other points raised in this discussion, indicate the need for further field work at Vik, a colony whose unusual features can elucidate the function of Puffin social groupings at more typical Puffin breeding sites.

3.8 MASS FLIGHTS AT THE BREEDING COLONY IN OTHER AUKS

Nine species in the family Alcidae are known to perform mass flights at the breeding colony throughout the breeding season (Table 3.26). The fullest descriptions of mass colony flights in another auk species are given in accounts of Little Auk (Plautus alle) behaviour (Ferdinand 1969, Evans 1981). In Ferdinand's study, Little Auks arriving at a Greenland colony in the pre-laying period circled over the sea, slowly approaching the coast as the size of flocks increased. At the colony the flocks fragmented, with smaller groups segregating to circle over different colony areas. Different circling flight routes were used by birds which frequented the sides of two different canyons at this colony. From observations of Little Auk flight routes and the temporal pattern of colony occupation, Ferdinand suggested that Little Auk breeding areas are divided into a number of sub-colonies, determined by topographic features.

Both Ferdinand and Evans commented on the loud calling of mass flying Little Auks, but Evans also noted a silent 'rushing flight' which rarely exceeded 50 individuals, these individuals possibly having taken off from a single location. Evans suggested that mass flights might maintain synchronisation of behaviour in Little Auk colony groups and help synchronise breeding within the colony.

Table 3.26 Incidence of mass flight behaviour at colony throughout breeding season in the family Alcidae (References on next page.)

Species	Latin name	Breeding range	Colony habitat	Peak daily colony attendance	Main documented predators	References
Little auk	Plautus alle	Arctic, Greenland to Russia	Boulder crevices on slopes sometimes inland	-	Larus hyperboreus, man	1,5,6,8,11,13, 18
Ancient murrelet	Synthliboramphus antiquus	N.Pacific	Burrows and boulder crevices	Sunset to sunrise	Falco peregrinus, man	3,4,6,10,16
Common Puffin	Fratercula arctica	N.Atlantic	Burrows and boulder crevices near sea	Evening	Larus marinus, man	This study
Horned Puffin	Fratercula corniculata	N.Pacific	Boulder crevices near sea	Dawn, dusk	Man	4,9,15,19
Tufted Puffin	Lunda cirrhata	N.Pacific	Burrows near sea	Dusk	Man	3,6,19
Rhinoceros auklet	cerorhinca monocerata	N.Pacific	Burrows in wooded areas near sea	Sunset to sunrise	?	6,7,12,14
Parakeet auklet	Cyclorrhyncus psittacula	N.Pacific	Boulder crevices near sea	Mid-day	Microtine rodents (nestlings)	6,17
Crested auklet	Aethia cristatella	N.Pacific	Boulder crevices nr. sea	Morning, evening	Man	2,4,6
Least auklet	Aethia pusilla	N.Pacific	Boulder crevices nr. sea	Morning, evening	Man	2,4,6

(P.T.O.)

References for Table 3.26

1. Bateson (1961) 2. Bedard (1969) 3. Beebe (1960) 4. Bent (1919) 5. Ferdinand (1969) 6. Kozlova (1957) 7. Leschner (1976) 8. Løvenskiold (1954) 9. Murie (1959) 10. Nelson (1970) 11. Norderhaug (1970) 12. Richardson (1961) 13. Salomonsen (1950) 14. Scott et al (1974) 15. Sealy (1973) 16. Saaly (1976) 17. Sealy and Bedard (1973) 18. Uspenski (1958) 19. Wehle (1976).

Due to the lack of data on mass flight behaviour in other auks it is not possible to suggest whether similar behaviour in different species may serve a similar function. All the auks which perform mass colony flights are, or have been, subject to predation at their colonies by avian predators or humans. As with the Puffin, predation is unlikely to be the sole reason for mass flight in the different species. For example, the occurrence of such behaviour in the nocturnal Rhinoceros Auklet (Cerorhinca monocerata) suggests that flight patterns in this species may be a result of birds attempting to synchronise movements to and from the colony with other auklets. The dense flock formations of Crested Auklets (Aethia cristatella) are visually reminiscent of Starling (Sturnus vulgaris) roost flocks and appear to involve the most complex mass flight manoeuvres of any auk species (see Sowls, Hatch and Lensink 1979, photo with Map 27).

Considering the flight behaviour of individual birds, there are similarities between Puffin Moth-flight and the 'Butterfly Flight' of Razorbills (Conder 1950, Bédard 1969, Birkhead 1976). This type of flight, which involves deep wing beats and glides, may be used by Razorbills departing from a cliff (Birkhead 1976). Conder (1950) described Butterfly Flight as a display seen most often in pairs of birds which left a cliff after mutual allopreening. Bédard (1969) felt that Butterfly Flight was used mostly by birds leaving precipitous cliff sites rather than sites near sea level, and that this behaviour was in part a function of colony habitat rather than a display.

Evans noted a type of 'butterfly' flight in pairs of Little Auks, the behaviour being observed only in apparently established pairs and possibly being associated with courtship. However, during early afternoon towards the end of the fledging period up to 90% of birds flying from the Little Auk colony could be engaged in this activity.

Storer (1952) described Common Guillemots (Uria aalge) leaving high cliff sites on Bonaventure Island using a slow flight with head and neck arched, but did not give a name to this behaviour. As with group flight behaviour, there is a need for comparative data on individual flight behaviour in different auk species.

The present study provides a framework for future detailed comparison of the structure and possible function of flight behaviour at the colony in different auk species, such data being absent from the literature to date.

3.9 GENERAL DISCUSSION - LINKS BETWEEN THE PRESENT STUDY AND OTHER STUDIES OF THE BEHAVIOUR OF PUFFINS AND OTHER VERTEBRATE PREY SPECIES

Diurnal Phasing of group movements to and from breeding places and roosting sites

Mass movements to and from breeding places are a spectacular feature of the behaviour of a variety of colonially breeding vertebrates. For example, Oilbirds (Steatornis spp.) and a variety of bat species fly out from breeding caves in large numbers at night to feed (e.g. descriptions in Attenborough 1979). Such behaviour could be considered as in part a response to the environmental stimulus of falling light intensity, rather than a specific grouping behaviour. Falling light intensity also influences the movement of some bird species to roosts, such as the Rook (Corvus frigilegus) (Swingland 1976). Given such environmental influences on the movement patterns of groups, could all movements of Puffins to and from the breeding colony be explained in a similar fashion, or was there evidence that movements of individual Puffins were in part determined by the behaviour of conspecifics?

Different species in the family Alcidae vary considerably in patterns of colony attendance. Most visit the colonies during the day, returning to the sea at night to roost if not incubating, although there is wide variation in the timing of colony attendance peaks between different species (Sealy 1972). Some species (Brachyramphus spp., Synthliboramphus spp., Ptychoramphus aleuticus and Cerorhinca monocerata) visit their colonies at night and spend the day feeding at sea. These differences in daily patterns of colony attendance may be due

in part to differences in the temporal availability of the various species' preferred food organisms in the sea. For example, P. aleuticus feeds on macroplankton which rise to the sea surface at night. However, this species is also subject to predation from Western Gulls (L.occidentalis) at some breeding sites, the gulls tending not to attack adult auklets at night (Manuwal 1979). Nocturnal colony visitation could thus also be related to predator avoidance, as has been suggested for another nocturnal species S. antiquus and for P. aleuticus elsewhere (Beebe 1960, Summers, cited in Sealy 1972).

The scarcity of Puffins ashore at the breeding colony during early mornings in the pre-laying period has been documented at a number of colonies (e.g. Lockley 1953, Myrberget 1959, Penicaud 1978). This could be due to the birds requiring time for feeding during the first hours of daylight before returning to the colony, as is suggested by Penicaud's (op. cit.) observations of peak Puffin numbers off a colony in Brittany at tidal high water in the pre-laying period. (Slater (1976) considered that colony attendance in Guillemots U. aalge peaked during flowing tides due to food availability being greatest around low tide.) However, Corkhill (1873) found no relation between feeding activity and tidal effects on Skomer, and no tidal influence on Puffin colony attendance has been recorded outside Brittany. My observations on the Isle of May, where landfall of Puffins at different island areas occurred at different times of day, further suggest that tidal cycles do not explain the phasing of Puffin colony attendance during the early part of the breeding season.

Differences in environmental conditions in different parts of a Puffin colony might influence when birds came ashore there. For example, flooding of burrows might necessitate delaying egg laying relative to laying in dry burrows (cf. Hornung and Harris 1976). Such variations in burrow environment do not explain variations within single day's attendance patterns at different colony areas, as observed on the Isle of May.

Various features of the behaviour of Puffins moving to and from colonies suggest that the movements of individual Puffins were in part a response to other Puffins. The increase in flight intention movements and erratic swimming observed during periods of water flock coalition is similar to increased levels of alertness and activity observed in some other social species before movement of groups. For example, in Canada Geese (Branta canadensis) head-tossing increases before group take-offs, and changes in vocalisations appear to help synchronise final take-off among group members (Raveling 1969). Jackdaws (Corvus monedula) also use different calls as signals of flight readiness, and an individual Jackdaw uttering such a call may fly up and land again repeatedly until its flock finally moves (Lorenz 1964). Data on moth-flying in Puffins has already been discussed, this behaviour being clearly associated with the synchronisation of movements from the colony by small groups of Puffins.

Thus various aspects of Puffin colony attendance within single days indicate that movement to and from different colony areas was associated with certain types of group behaviour, such as water flock merger, wheeling and moth-flying at or near these areas, and that such behaviour was not simply

a response to environmental stimuli such as tidal changes or light intensity.

Variations in Puffin colony attendance over longer periods cannot be readily explained by any data presented here or by previous workers. Peaks in attendance every few days have been documented at a number of colonies, the periodicity varying between different localities. For example, peaks were noted every four to seven days on Skomer and on Great Island, Newfoundland, but every four to 11 days on Lovunden (Myrberget 1959, Corkhill 1970, Nettleship 1972, Lloyd 1972, Ashcroft 1977). Attempts to relate this apparent periodicity in attendance to weather conditions have been largely unsuccessful. Myrberget (1959) found a possible link between the number of birds ashore and sea conditions, with fewer birds ashore when there was a heavy swell. Brooke (1972) found a slight association between higher Puffin numbers on the Shiant Islands and low wind speeds, but Dott (1974) found that both calm, sunny weather and stormy weather coincided with high Puffin numbers on Dun. The highest Puffin numbers ashore on Boreray, St Kilda, during 18 days in July 1980 were on a day of severe gales, rain and mist (pers. obs.). Changes in the number of Puffins ashore on Skomer appeared quasi-cyclic in one study, being chiefly but not entirely related to the numbers there the day before (Ashcroft 1977).

Peaks in colony attendance every four days on the Isle of May in the present study were thus in accordance with previous studies of pre-laying period colony attendance, but the reason for such periodicity in behaviour remains obscure.

Puffin colonies as 'Information Centres'

The hypothesis that communal roosts and communal breeding sites may function as 'information centres', where individuals exploiting a patchy or otherwise unpredictable food source may capitalise on other individuals' knowledge of feeding locations (Ward and Zahavi 1973) has already been mentioned in discussion of Puffin departures from wheels. Ward and Zahavi (op. cit.) considered that wheeling was a colony advertisement display, serving the function of attracting as many Puffins as possible to a breeding site. These authors suggested that such behaviour could increase the amount of information about feeding locations available to individual Puffins at a colony, transfer of information possibly occurring at 'meeting places' away from burrows. Skokova (1962, 1967) suggested that such information transfer might take place in the wheels themselves, or otherwise that wheels 'connected' colonies to adjacent feeding grounds.

I disagree with Ward and Zahavi's interpretation of wheeling for a number of reasons. Data presented in this study indicate that wheeling was in part associated with movements of Puffins from the sea to a breeding site and vice versa. In the pre-laying period, such movements mainly took place from late morning onwards, possibly after Puffins had fed. If such birds did not feed again until the next morning (as was apparently the case for many individually marked birds monitored at the colony), there would thus be a lag of some 15 hours or more between wheeling and feeding. Unless shoals of prey fish stayed in the same position over such a period, information received from other Puffins in a wheel about fish location would be equivalent to 'yesterday's news', and of

little use on the next foraging trip. Before the main arrival of immature Puffins at a colony in the incubation period, the population of Puffins visiting a colony is made up of potentially breeding birds, the bulk of which arrive en masse at the colony in late March or April. During this period the term colony 'advertisement' thus seems a complete misnomer for the behaviour of a population which has already 'bought' the commodity being advertised. Later in the season, wheeling activity often peaks in the evening in fading light conditions when such behaviour is likely to be invisible to birds outside the immediate vicinity of the colony. Ward and Zahavi's interpretation of wheeling thus seems highly implausible.

Given these reservations, and earlier reservations about interpretation of clumped landings from wheels, could the Information Centre Hypothesis have any relevance to understanding Puffin group behaviour? I suggest that it could to a limited extent, but feel that no study of Puffins to date has produced data adequate for such an assessment. The hypothesis is likely to be of limited use in describing group behaviour throughout the day, for the simple reason that from shortly after dawn onwards, the general direction of fishing grounds relative to a Puffin colony is usually quite evident, even to a human observer, on the basis of 'flight lines' of birds flying to and from fishing grounds. The phasing and direction of departures of Puffins from small areas of a colony in the early morning could merit further studies, some observations presented here indicating that not all Puffins leave the colony in the same manner, with some delaying departure more than others. Data showing whether such delays were associated

with feeding performance would be one means of assessing whether individual Puffins do indeed monitor the feeding performance or behaviour of others in the colony, but even data of this type would constitute only circumstantial evidence for information transfer. As discussed by Loman and Tamm (1980), the Information Centre Hypothesis cannot be considered a testable hypothesis in the strict sense. It is possible that certain types of communal behaviour, such as communal roosting, or in the case of Puffins, grouping on foraging trips, could have a number of advantages which have led to the evolution of the behaviour. Given the possibility that not all such advantages need be simultaneously present during the performance of such behaviour, the hypothesis thus constitutes one of several complementary explanations.

The reaction of prey groups to predators

As discussed by Treisman (1975) two main accounts of how predation may have an effect on group behaviour have been put forward since Darwin (1859) suggested that predation could be a factor limiting animal numbers, and further suggested that there could be selection for 'sympathetic' tendencies in predator avoidance (1888). The first set of accounts relate to how animals should divide their time between eating and watching for predators in foraging groups and has already been discussed (Final Discussion, Chapter Two).

The second set of accounts postulates that grouping in prey serves to conceal individuals in such groups from predators. An influential concept in this context is the idea of such a group being a 'selfish herd', where an animal with near neighbours in a group has a smaller 'domain of danger'

from predators than a solitary animal (Hamilton 1971). Such defensive hiding tactics have been particularly invoked in discussions of schooling behaviour in fish (e.g. Williams 1964, Breder 1967). Hamilton assumed that a predator always caught the nearest prey and that there was no confusion effect. This was not the case with gull predation on Puffins. Hamilton's model also fails to adequately describe the behaviour of some other predators, such as the Three-spined Stickleback (Gasterosteus aculeatus L.) which does not preferentially attack the nearest prey in Daphnia swarms (Miliniski 1977 b).

Wheeling Puffins flew closer together when a hunting gull was in the vicinity than at other times. Such bunching of prey in response to a predator is a widespread phenomenon amoung vertebrates which form groups. Indeed Lorenz (1967) felt that there 'is not a single gregarious animal species whose individuals do not press together when alarmed, that is, whenever a predator is close at hand'. Striking examples of this type of behaviour are the defensive circle behaviour of the Musx Ox (Ovibos moschatus) and the tight clustering of Starling (Sturnus vulgaris) flocks in the presence of aerial predators (Horstmann 1953). Several authors have suggested that predation may have been a selective force influencing avian flock formation (reviewed by Moriarty 1976).

For many species of schooling fish, the structure of schools also changes in the presence of predators, the fish tending to swim closer together and in one direction (Parr 1927, Breder 1959, 1967, Shaw 1970, Radakov 1973, Major 1977, 1978). A number of authors have suggested that such behaviour could be advantageous for individual fish if their predators were

subject to a confusion effect (see this study, Final Discussion, Chapter Two).

Features of schools or invertebrate swarms which have been shown to influence predator attack success through a postulated confusion effect are the number of prey in a school (Neill and Cullen 1974); swarm density (Milinski and Curio 1975) and uniformity of swarm members (Oguchi 1978). In this context, the behaviour of Puffins in the presence of a hunting gull would seem an appropriate defensive strategy, and is analagous to the defensive behaviour of schooling fish.

Data indicating that clustering of Puffins in a wheel increased with increasing numbers of Puffins in the wheel are also paralleled by data on fish school structure. Varying the number of fish in schools of minnows (Phoxinus phoxinus) affected their three-dimensional structure and internal dynamics, the distance between fish decreasing as the number of fish increased (Partridge 1980). Other authors also consider that schools are better integrated if there are more fish in them (Schlaifer 1942, Narsall 1973).

For actively swimming schools, Partridge (1980) suggested that internal structure may be fairly constant, and further suggested that when schools form they may need to satisfy certain criteria of inter-fish spacing and three-dimensional structure. This could lead to close similarities in the structure of schools of a wide variety of species. Parallels drawn here between the behaviour of wheeling Puffins and the behaviour of schooling fish suggest that such ideas may also have a bearing on the study of avian flock formations. More detailed investigation of the structure of Puffin wheels in

the presence and absence of aerial predators, possibly using stereoscopic photography, would thus be a logical and potentially fruitful extension of the present study.

CONCLUSION

Implications of the present study for the management, monitoring and future study of gulls and Puffins

CONCLUSION

Data on interactions between gulls and Puffins on Dun indicate that in future years the number of Puffins killed by gulls on the island is unlikely to increase above the level recorded in the present study. The Dun Puffin colony as a whole should thus not be seriously depleted by the continued predatory activities of gulls breeding there. Gull predation may cause a decline in the small number of Puffins breeding in the Sparse sub-colony area. With further depletion of Sparse Area Puffin numbers, this part of the colony may cease to be a suitable source of food for supporting gulls throughout the breeding season, and regular predation may stop before extinction of the sub-colony. Further studies of the ranging behaviour of gulls on Dun, using colour-marking and radio-telemetry in addition to techniques employed in the present study, would be useful to assess the possible long-term effects of gull predation on the Sparse Area.

If those bodies responsible for the management of St Kilda as a National Nature Reserve consider that further studies indicate an unacceptable depletion of the Sparse Puffin sub-colony due to gull predation, some form of gull population control may be deemed necessary. Data from the present study suggest that such control measures should be restricted to the Sparse Area. Shooting of gulls early in the breeding season would be inefficient, since other gulls could move in to cleared areas and establish hunting ranges. Prudent management might be to prick eggs in Sparse Area nests. Pairs of gulls incubating these eggs should continue to defend hunting areas against other gulls during the incubation period, only catching Puffins to the limited extent normal during this part of the

breeding season. If such gulls abandoned their breeding attempt late in the incubation period, other gulls might have insufficient time to move in and raise chicks by exploiting the hunting range of the failed pair. Field experiments on the effects of such egg manipulation should be conducted to assess the efficiency of such a control measure.

Data on Puffin grouping behaviour indicate that the spatial distribution and numerical strength of some groups, such as water flocks and wheels, reflects the geographical extent of sub-colony areas and may give an index of the number of Puffins breeding in a sub-colony. If counts of Puffins in water groups and in wheels are made early in the breeding season, before the influx of immature Puffins, such counts may be of use in determining the numbers of Puffins breeding in sub-colonies where nests are inaccessible. This technique would be particularly useful in habitats such as boulder scree or boulder beach, two typical Puffin breeding habitats in the north of the species' range. Preliminary work to assess the accuracy of such a technique could be conducted at colonies with well separated sub-colony areas where sub-colony populations can be determined using conventional counts of burrow occupancy.

By joining water flocks and wheels individual Puffins can synchronise some of their movements to, from and within a breeding colony with numbers of other Puffins. This study indicates that joining such groups could reduce an individual Puffin's risk of predation if the groups are large enough to reduce predator hunting efficiency through a confusion effect. Participation in such groups could have other benefits not documented in the present study. Since groups are associated with sub-colonies, synchronisation of sub-colony attendance could help synchronise other activities within the sub-colony,

noteably the breeding of Puffins in neighbouring burrows. Data on wheeling behaviour and colony attendance in the Sparse Area suggest that aerial grouping behaviour may be ineffective in synchronising colony attendance under some circumstances in sub-colonies where burrow density is low. This breakdown of group behaviour could in turn influence the spread of egg laying in such an area, increasing an adult Puffin's risk of losing fish to kleptoparasites and making newly fledged young more vulnerable to predation. Since immigration to such an area might be inhibited by the absence of large groups of Puffins on the ground, the sub-colony would decline. Further fieldwork at low burrow density Puffin colonies would be useful to test these hypotheses. Data from the present study support the idea that Puffin grouping behaviour is most effective in synchronising movements of birds in and around sub-colonies when these sub-colonies contain large numbers of breeding Puffins. Data on the hunting behaviour of one of the Puffin's major predators, and ideas in the paragraphs above, further suggest how there could be selection pressure leading the majority of Puffins to breed in large, high density colonies.

This study leaves many questions unanswered. I hope that it provides a framework which will allow some of the intricacies of social behaviour in the Puffin and other auk species to be further unravelled in the future. I trust that it will also be of use in the monitoring and management of Puffins and their predators on nature reserves. The Puffin wheel over the Dun summit slope may appear to be like St Kildan Roulette, where the loser pays the ultimate price, but the odds are good that the wheel will keep spinning for years to come.

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APPENDICES

APPENDIX 1

Puffin social behaviour at the breeding colony
(Written as a chapter for a forthcoming general readership book on Puffins by Dr. M.P. Harris)

Puffins use a variety of displays and postures in their social life at the colony. While some displays, such as those associated with mating and pair-bonding, are quite obvious to the human observer, others are more subtle. A catalogue of puffin behaviour is given here to serve as a brief guide to puffin society. The descriptions are based on observations of individually colour-ringed puffins of known breeding status and sex on the Isle of May. Some of these displays have previously been described by Perry (1946), Lockley (1953) and Myrberget (1962).

Courtship and pair-bonding behaviour

Head-Flicking with Wing-Flutter

This behaviour is performed by the male puffin in the vicinity of a female as a precursor to copulation. In the first phase of the display, the head is thrown sharply up, back, and down again with mechanical regularity at the rate of at least one throw per second. As the displaying male approaches the female, he raises his chest and begins to flutter his wings in short bursts, still Head-Flicking. If the female allows a close approach, the male's wing fluttering becomes continuous, and he mounts the female for a few seconds to copulate.

The display is seen most often in rafts of puffins on the sea prior to egg-laying. Often the female dives or takes off, then the male may approach another female and repeat the display. A single male once displayed to seven different females in 20 minutes (Myrberget 1962). When mated, paired puffins may swim closer together in the rafts than un-paired birds (Corder 1950).

Head-Flicking/Wing-Flutter is sometimes seen on land, but although the male may succeed in mounting the female briefly, copulation is not usually successful. Wing-Fluttering with occassional Head-Flicking may also be used by the male

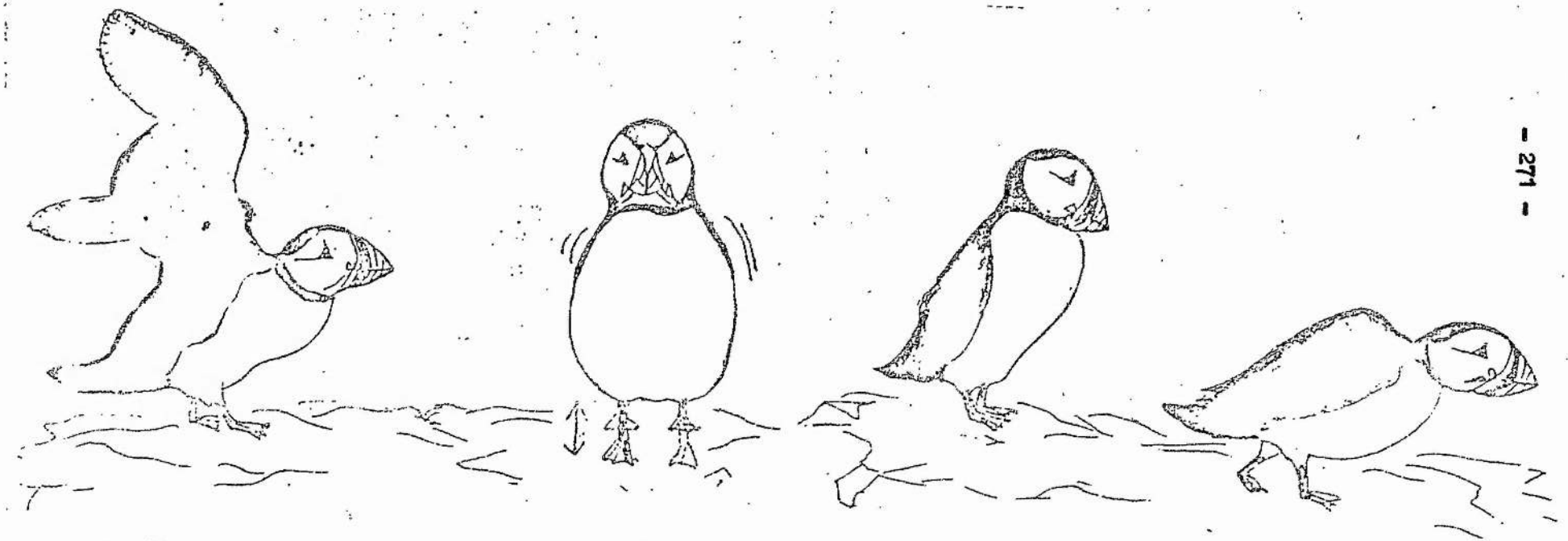


Fig. A.1 Landing Posture and three locomotory/ritualised locomotory postures used by Puffins at the breeding colony

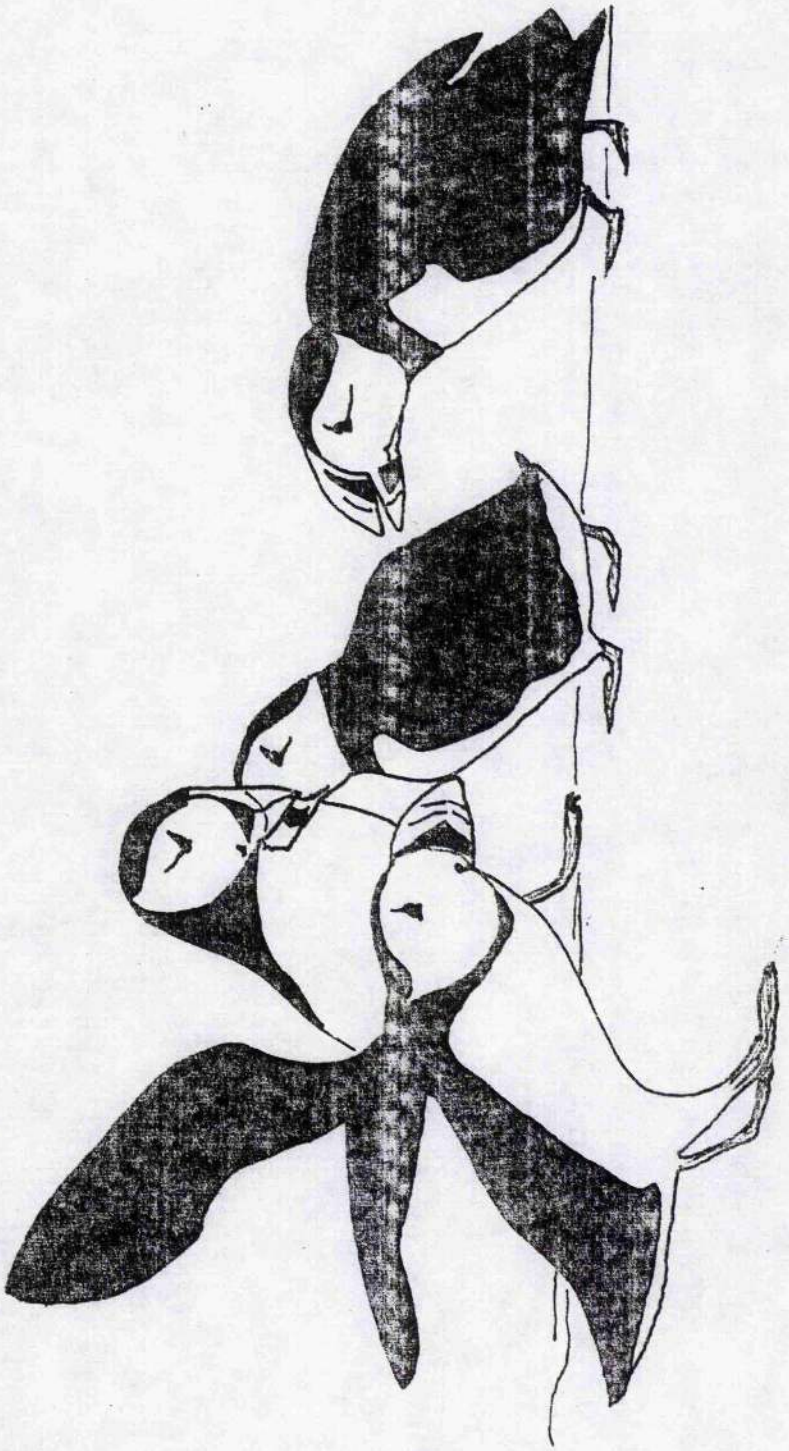


Fig. A.2 Pair of Puffins Billing, with onlooker exhibiting Aggressive Gape and near lander showing Landing Posture

to coax a female to a burrow.

The female puffin has no special mating display. She merely tolerates or rejects the advances of the male.

A similar type of Head-Flicking is used in the courtship display of male tufted and horned puffins (Wehle 1980). In the guillemot, Head-Throwing is a female behaviour seen before copulation.

Billing (Fig A.2)

Mainly associated with pair-bonding, Billing (Figure 4) is a very obvious and noisy puffin activity, occurring on both sea and land throughout the breeding season.

At the start of a bout of Billing on land a puffin of either sex makes a low profile approach (see later) to another, often its mate. The approaching bird swings its bill from side to side, and may nuzzle or nibble under the other's bill. The two birds then begin to knock their bills broadside together. This may last from a few seconds to a minute or more. During the Billing one bird often adopts a high profile posture with neck and head feathers raised and the bill angled down, while its partner maintains a lower profile with more sleeked feathers. Both birds cock their tails and pad slowly round on the spot with toes splayed. On the sea, Billing birds tend to pirouette in the water as the bills meet near the sea surface.

The noise of clashing bills can be heard several metres away, and Billing often attracts the attention of other puffins in the vicinity, which rush over and stand close to the displaying pair. A prolonged bout of Billing may draw a large audience of ten or more puffins encircling the Billing pair. The onlookers

are not always content to be passive spectators, but may themselves attempt to nibble the beaks or feathers of the Billing birds, and some bouts end in a fight between a displayer and a spectator. Sometimes one of the initial pair breaks off Billing but immediately starts again with one of the onlookers.

As well as stimulating the interest of bystanders, Billing often has a contagious effect on other pairs in the vicinity, so that it is not uncommon to see several Billing pairs with associated bystanders simultaneously in a small region of burrow slope. At the end of a Billing bout, one puffin often keeps swinging its head from side to side for several seconds after its partner has lost interest. Some nibbling of the fleshy yellow gape rosettes may occur at this point. This is reminiscent of the allopreening often seen following Billing in the razorbill but which is absent from puffin behaviour.

Billing is stimulated by a variety of events, such as the landing of a bird near its mate, a fight near a pair, or another puffin just passing by. Although a characteristic interaction between puffins in a mated pair, some features of Billing, such as its attractiveness to onlookers and its often 'promiscuous' nature, suggest that it may have a wider significance than just a pair-bonding behaviour.

Bowing

Though it is seldom seen, Bowing is performed by both sexes. In one form it appears to be an invitation to start Billing whereas without head movement it may be a threat display. (Myrberget 1962)

On land, a Bowing puffin stands with its head bent down almost to ground level, this sometimes giving the bird the appearance of trying to look backwards through its own legs. The head and neck feathers are raised, and the head turned

slowly from side to side, the posture being held for up to a minute. On the sea, the beak is bowed down to the water surface, and the posture is mostly observed in association with the male's pre-copulation display.

Threat and fighting behaviour

Gape (Fig A.2)

Gaping is used as a threat by both sexes, and has a range of intensities. bill is held slightly open, the tongue may be raised and the neck feathers erected with increasing threat intensity. A brief Gape, where the head is angled towards the bird being threatened, is frequently seen in communal grouping areas, directed at a bird which has landed nearby. The Gaping bird often follows the threat with a swift bite at the lander. In this situation, the threatened puffin usually moves off, but in burrow areas a Gape by one bird is commonly returned by the puffin being threatened. The two birds then face each other, Gaping and turning their heads. This is a Gape-Contest, a high intensity mutual threat display.

Gape-Contest

The contestants' beaks are angled up slightly, opening and closing slowly, and often synchronously. Head and neck feathers are erected, tongues raised, and a low 'creaking' call is uttered (Lockley 1953). The birds avoid eye to eye contact by turning their heads in such a way that each bird turns to its left and right in unison with the other. The whole performance has a slow motion appearance, and the yellow mouth lining is vividly displayed during each Gape.

Fight

One bird in a Gape-Contest usually stops Gaping after a while and hurriedly moves or flies off, but if not, a full fight can develop.

In a classic fight the assailants face each other with feathers stiffly raised and wings outstretched. They interlock beaks and wrestle with twisting head movements. The outstretched wings are alternately pressed to the ground for balance and used as flails to buffet the opponent, and the feet claw upwards like grappling irons . In some fights, one bird may grab the other by the scruff of the neck, or by the wing. In these circumstances the puffin being bitten usually tries to break free from the outset, and the fight is not so much a contest as a one-sided struggle to escape. A loud growling call is given by fighting puffins, and is often the first indication of aggression noticed by the human observer. Fighting puffins often become so intertwined that they tumble as a single furious ball of feathers down the burrow slope, occassionally even overshooting the cliff edge still locked in combat. Fights can end many metres away from their point of origin with one bird rapidly breaking from the tustle and flying off. If the 'victor' is far from its burrow it may become involved in further threatening or fighting while walking back to its own burrow.

Fighting is a popular sport among puffins, groups of a dozen or more forming around prolonged contests. Although noisy and sometimes prolonged I have never seen a fight result in severe injury, as happens in some other seabirds (Nelson 1978), but some contestants leave fights with a bleeding gape.

Fighting is often associated with burrow defence, and even a shallow scrape being excavated by a young pair in the season before they breed will be defended vigorously. The frequency of fights is highest in the evening, partly because

there are more birds ashore at this time, but more importantly due to the increased ranging behaviour of individual puffins around dusk (see below).

Stylised walking

Due probably to the great development of chest and leg muscles for swimming and digging, the puffin has a rather 'rolling' gait in any situation. The Normal Walk, where the body position is neither stiffly upright nor depressed, is used most often when the density of standing birds on rocks and between burrows is low. When the density of standing birds is higher, two other forms of walk are frequently used. Each functions both as a means of locomotion and as a display.

Low-Profile Walk

The body is held horizontal close to the ground (Figure A.1) and the head held more in line with the back than in the Normal Walk. The carpal joints are raised, giving the body a slightly 'hunchback' appearance. Birds using this walk tend to move rapidly in brief spurts, stopping to rise up and look around before moving on.

The Low-Profile Walk is used at all times of the day by birds which are moving outside their own burrow territory. There is a dramatic increase in its frequency around dusk as more and more birds begin to move around investigating many burrows in their part of the colony. The Low-Profile Walk posture, which is the antithesis of the upright Gape threat or Fight posture, and the context in which the walk is used, suggest that it serves to reduce aggression while birds are moving outwith their own burrow territory. To near standing burrow owners the walk might signal 'I'm just passing by and mean no harm'.

Pelican Walk

In contrast to the Low-Profile Walk, the Pelican Walk posture is stiffly erect (Figure A.1). The head is lowered to touch the puffed breast feathers and the tail often raised. Foot movements are slow and stylised, each foot being raised and lowered in turn in an exaggerated manner, as if the bird were treading on hot coals. This is reminiscent of 'parading' in some boobies.[256] This walk is most often used by a bird near its burrow, where it may take a few Pelican Walk steps often circling the burrow entrance, after its own landing or after another puffin has passed or landed nearby. It is also sometimes used by a puffin approaching another prior to Billing.

This walk is a site ownership display which may serve as a mild threat, often to near passing Low-Profile walkers. It is intriguing to think that puffins can conduct silent locomotion dialogues, where the status quo is maintained by each walker adopting a body posture appropriate to its position relative to its home burrow.

Spot-Stomp (Fig A.1)

Although not actually a locomotory behaviour, this may have been ritualised from moving postures during evolution. In Spot-Stomping, the puffin raises and lowers alternate feet with the webs spread several times in succession while remaining on the one spot.

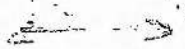
Spot-Stomping is a frequent response to a near landing, and is also used by burrow owners on the near passage of another bird. Again it signals site ownership - either of a burrow or of space on a grouping area.

Stylised foot movements, as in the Pelican Walk and Spot-Stomping, may have led to the evolution of the puffin's bright orange-red foot colour due to selection

for good visibility of display signals.

Stylised flying

Moth-Flight

In Moth-Flight  , a puffin takes off from the colony and angles its wings more upwards from the body than in normal flight, movement being powered by rapid fluttering of the wing tips and by gravity. The body is arched with the head angled down, and the feet often crossed. Moth-Flight cuts the puffin's airspeed to about half normal flight speed. It is used by both sexes, and is a final signal of a bird's readiness to depart for the sea.

It is sometimes the main flight seen over the burrow slopes at dusk. At this time singleton Moth-Flyers which are not joined by other birds in the air tend to track in a wide loop around the burrow slopes and land at the colony again. The bird repeats this performance until it is joined in the air by one or more other puffins. They then head out to sea together and in most cases do not return to the colony that night. I have seen members of known breeding pairs synchronise their evening departure to the sea in this way.

The razorbill also uses a Moth-Flight but this is used throughout the day.

'Comfort' behaviour

Puffins use a number of behaviour patterns, such as preening movements, for bodily maintenance. In some contexts certain of these patterns may also indicate the motivational state of the bird, for example its readiness to take flight. Comfort behaviour patterns with this dual aspect are as follows.

Rise-Up/Wing-Shake

In this behaviour, normally used on land and sea to settle the feathers, the puffin raises its chest, fluffs its body feathers, beats its wings briefly, shakes its tail then settles down again. On the sea, the chest rises well clear of the water surface.

Head-Dip

This is a brief submersion of the head, often repeated many times in quick succession.

Both Rise-Up/Wing-Shake and Head-Dip can be used as 'displacement' behaviour - a kind of redirection of nervious energy - signifying that the puffin is anxious to take flight, but unwilling to do so alone. The frequency of these behaviour patterns increases greatly when birds in a water-raft are about to take off and move to the land. Bill-Dipping in the black guillemot is also a displacement activity which indicates nervousness (Asbirk 1979).

Head-Shake

A rapid side to side head movement, used to shake water from the bill, this behaviour can also be used to indicate site ownership. A higher proportion of puffins landing at their burrow Head-Shake soon after landing than birds landing on other areas.

Other behaviour

Landing posture

This is seen when a puffin lands near other puffins. The body is kept horizontal, the legs partly bent, the wings held above the back, and the feathers slightly sleeked (Figs A1, A2) The head is often angled up, and one foot may be

placed prominently in front of the other.

A puffin landing away from other puffins folds its wings immediately. A puffin landing close to a bunch of others may keep its wings raised for three seconds or more, even although it has space to fold them. In general, the closer a puffin alights to another puffin, the longer it maintains the landing posture.

This posture is an 'appeasement display' - that is, it functions to reduce or inhibit attack in conditions where escape is disadvantageous (Manning 1978). A puffin may gain advantages from joining a group, such as increased protection from predators. It would lose these advantages if it were forced to take off again by an attack from a group member. The landing posture 'appeases' near standers and helps the lander stay in the group without disruptive aggression.

Milling

This is an erratic to and from swimming movement, usually preformed by small groups of neighbouring birds in dense water rafts close inshore. The head is held high and the back sunk low in the water, giving Milling birds the appearance of stretching their necks upwards.

Flocks on the water often drift near the shore shortly before the raft birds take off to occupy the land. Milling may indicate pre-flight excitement before birds move to the land during the day, or fly farther out to sea in the evening. Myrberget , who called this behaviour the 'water-dance', saw it most commonly at dusk in Norway.

Wheeling

This is flight in a broad elliptical track - the Wheel - above a small area of the breeding colony. It is most noticeable when performed simultaneously by large numbers of birds. The birds fly into the wind over land, turn sharply at the end of a few hundred metres, and fly with the wind offshore or on to the outer Wheel track before turning in again to complete the circuit. In moderate to strong wind most Wheeling birds make a figure of eight air loop at one or both turn points. Each Wheeling puffin flies in a land track roughly over its own part of the burrow slope, so that for example a bird flying high in the Wheel will tend to land at a high burrow area. Individuals normally make only a few Wheeling circuits before landing or heading out to sea. At large colonies the heavy traffic of birds to and from Wheels maintains numbers in the air, and can give the impression of incessant roundabout flying. Wheeling is a virtually constant feature of some large colonies. The number of birds in a Wheel tends to be greatest in the evening, when individuals, often using the Moth-Flight before joining a Wheel, may make repeated circuits and landings at the colony before flying out to sea.

Wheel turn points are often above geological features, such as gullies, which demarcate sub-areas of the puffin colony. Each sub-colony has a distinct Wheel track which varies little from year to year.

Wheeling is used for reconnaissance of a burrow area before a bird lands. It allows reasonably synchronous occupation of small areas of burrows, since each puffin in the Wheel is often flying near its close colony neighbours and can quickly follow any landings at its own part of burrow slope. Wheeling is also a signal of a bird's readiness to land, and may encourage birds in nearby water flocks to join it, again helping synchronise colony occupation.

Head-Jerking

The body is stretched upright and the feathers may be sleeked while the puffin Head-Jerks. The head is thrown back at a shallower angle than in male Head-Flicking, and there may be some lateral head movement. Head-Jerks are performed at the rate of one per second, or slower, in bouts which may last several minutes. The behaviour can be performed by static or moving birds, by singletons or by large groups simultaneously. A monosyllabic call - 'uh .....uh .....uh .....' - is uttered once for each backward jerk of the head.

Whilst Head-Flicking as part of the male's pre-copulatory display is usually seen on the sea in the spring, Head-Jerking is performed on land by both sexes throughout the breeding season.

Although Head-Jerking can be seen from time to time throughout the day, the frequency and intensity of the behaviour increases around dusk. In this period, it is not unusual to see every puffin on a burrow slope Head-Jerking, and at this time the behaviour is frequently associated with Low-Profile Walking. My interpretation of this display is that it in part signals the readiness of a bird to leave for the sea. It may stimulate similar excitement in other puffins nearby which culminates in mass Head-Jerking and eventually in the reasonably synchronised departure to the sea of puffins from one small part of a colony. The call must be audible underground as it is also used by adults to encourage their chick out of the burrow to exercise its wings in the evenings prior to fledging. At dusk, groaning calls by birds underground increase, perhaps stimulated in part by Head-Jerking calls from above ground.

Head-Jerking may be interspersed with brief bouts of Gaping, and in some periods is performed more by males than females. As with Billing, Head-Jerking is a complex social behaviour which deserves further study.

Looking Down Burrow

Defined by its context, this action is nevertheless quite a distinct behaviour which can be used as a social signal. The bird stands at a burrow entrance and peers down the hole, periodically raising its head to look around before looking down again.

When performed by one bird near its mate or prospective partner, this behaviour signals the bird's readiness to go down the burrow and is used to encourage the partner to join it. Yet again at dusk the behaviour is used more generally in conjunction with Head-Jerking and Low-Profile Walking as part of the wider evening reconnaissance of several burrows. A breeder looking down a neighbours burrow may receive a sharp jabbing attack from the burrow owner. This partly explaining the increase in fighting around dusk. Immature puffins without mates investigate many burrows in this way throughout the day, and are often attacked as a result.

Puffin watching

The descriptions above indicate the main features of puffin behaviour which can be observed at the breeding colonies, but some comments on the tempo of puffin social life may help puffin watchers.

In the pre-laying period, much of the puffin's social activities take place in water rafts and are visible only through a good telescope.

In the incubation period, the birds spend more time ashore, but the extent of colony visitation is variable, both within and between days. Even on a day when many puffins are ashore, there may be long periods of inactivity on the burrow slopes when most birds are merely sitting, preening or sleeping. More exciting behaviour tends to occur in bursts - a pair begins Billing some spectators rush over, a fight breaks out, a gull flies over and panics the slope to flight, the puffins land again and settle down, to sit, to preen, to sleep.

Once the chick hatches, the adult puffins spend much of the day flying to and from the fishing grounds, but by then the summer influx of immatures has occurred, and there will usually be at least a few birds ashore at the colony. Immatures spend much of their time loafing, but are also inquisitive and eager to try out their social skills, so many behaviour patterns can be seen throughout the day. In general though the best time to watch puffin behaviour is in the evening during the chick-rearing period. At this time, many of the breeders will have finished fishing, and on a good landfall day the immatures birds will swell the ranks on the burrow slopes. An observer sitting quietly in a good vantage before sunset can see many behaviour patterns, and watch the suite of Head-Jerking/Fighting/Low-Profile Walking/Burrow-Visiting and Moth-Flying behaviour gradually unfold as areas of the slope begin to be abandoned in the fading light.

Despite the inevitable waiting, cold limbs, and eye-strain, the experience of watching this feverish colonial activity more than compensates for the discomfort.

APPENDIX 2

A selection of recent publications by the author based on work carried out during the period of the present study

(Seabird Report (1982))

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Notes on the robbing behaviour of Arctic Terns at Puffin colonies

by K. Taylor

INTRODUCTION

The Arctic Tern (*Sterna paradisaea*) usually feeds by fishing over water. Whilst various members of the Laridae and Stercorariidae commonly obtain fish by kleptoparasitism (Brockman and Barnard 1979) or by gleaning fish dropped on the ground at Puffin (*Fratercula arctica*) colonies, such behaviour is unusual in Arctic Terns, having been recorded regularly only on the island of Mykines in the Faroe Islands (Williamson 1948, Nørrevang 1960). Puffins do not eat fish which they drop either accidentally or after being attacked by a kleptoparasite, and kleptoparasites do not always find all fish dropped by a Puffin after a successful attack. Such fish is thus available as food for birds of other species even if these were not the original protagonists. Feeding on dropped fish in this manner is referred to here as 'gleaning'. 'Pirate' is equivalent to 'kleptoparasite' throughout this paper. These notes extend previous accounts of inland foraging by terns on Mykines, and describe tern foraging behaviour at an Icelandic Puffin colony. This leads to consideration of why tern foraging at Puffin colonies is uncommon.

Elsewhere, the Arctic Tern is not widely recorded as a kleptoparasite of other birds. It has been seen robbing fish from Puffins south of Puffin Island, Co. Kerry and off the Farne Islands (P. G. H. Evans and M. P. Harris pers. comm.); from Black Guillemots at Aedey and Flatey in Iceland (Bardarson 1975, A. Petersen pers. comm.); and from Horned Grebes in Iceland (Bengston 1966).

STUDY SITES

(1) *Mykines* (62°07'N, 7°38'W) is the westernmost island in the Faroes. Puffins breed along much of the Mykines coastline (Nørrevang 1977). Puffin burrow density in the colony areas between Mykines village and the holm Mykinesholmur, a distance of about 750 metres, is up to four burrows per square metre (pers. obs.), one of the more than 50,000 pairs of Puffins bred in these areas in 1979. Nørrevang (1960) estimated that about 1,200 pairs of Arctic Terns bred on Mykinesholmur, at a site less than a kilometre from these Puffin areas, in the 1950's, and stated that Herring Gulls (*Larus argentatus*) were the main pirates of Mykines Puffins.

(2) *Vik i Myrdal* (63°25'N, 19°30'W) is a township close to the southernmost point of Iceland. Puffins at Vik breed inland at two cliff sites, separated from the sea by a glacial outwash plain. The Vik East Cliff Puffin colony lies about one kilometre inland. Puffin burrow distribution at this site has been described by Grant and Nettleship (1971). The total number of Puffins breeding at the East Cliff is of the order of thousands of pairs (the topography makes burrow counting dangerous), and burrow density is lower than at the Mykines study site. Puffins flying to the East Cliff with fish to feed their chicks are attacked by a number of pirates, principally Arctic Skuas (*Stercorarius parasiticus*), Herring Gulls and Lesser Black-backed Gulls (*Larus fuscus*) (Grant 1971, Arnason 1978, Arnason and Grant 1978). The latter two species, and others such as Kittiwake (*Rissa tridactyla*) and Raven (*Corvus corax*) are also gleaners at the East Cliff. Arctic Terns breed within one kilometre of the East Cliff in a colony of a few hundred pairs, seawards of the cliff.

METHODS

Terns were observed at Puffin colony areas near Mykines village between 19 and 23 July 1979, and at the Vik East Cliff between 13 and 16 August 1979. Since my main study at both sites concerned Puffins, tern observations were casual rather than systematic. Notes on Mykines terns were mainly observations of patrolling behaviour. At Vik, individual terns flying near the East Cliff were watched from their arrival at the cliff until they flew out towards the tern colony after patrolling near the Puffin colony. Tern patrol duration, foraging success and interaction with other birds was noted.

RESULTS

Tern patrol times and gleaning success are illustrated for both sites in Table 1. Fish found on the ground at both sites were Sand-eels (*Ammodytes marinus*). Gleaning success was much lower at Mykines (11%) than at Vik (48%).

TABLE 1. TERN PATROL DURATION AND GLEANING SUCCESS.

Site	*Mean patrol time (secs)* ± SE					
	Successful	*n*	*Unsuccessful*	*n*	*Total*	*Success (%)*
Mykines	15.0	1	184.4 ± 73.3	8	9	11
Vik	120.8 ± 44.4	12	108.6 ± 23.4	13	25	48

The normal tern patrol at Mykines was a rapid zig-zag traverse of a Puffin slope, sometimes pausing to hover near the ground. Not all hovers resulted in a bird securing a fish. Flight height was about two metres. Single patrolling birds chased off another tern which flew within ten metres of the patrolling bird in three out of nine patrols monitored for patrol duration and gleaning success. Other chases were seen in more casual observations. Up to three terns were seen simultaneously quartering different areas of the same burrow slope (c150 m by 250 m). Once, when a Herring Gull forced a Puffin to drop a fish load, three terns flew over to the site and chased off the gull. The terns then squabbled over the remnants of the dropped load. Another isolated observation was of a tern which began to hover at a Puffin burrow entrance just before the burrow owner landed with a fish load. The tern dived towards the Puffin, which dropped the fish and bolted down the burrow. The tern then picked up a fish and flew off to a nearby nest. Fish obtained at the Puffin colony were always carried to a tern breeding site.

At Vik, Arctic Terns were seen quartering the lower burrow areas at the East Cliff and gleaning fish on all days of study. As on Mykines, patrols were rapid low level zig-zags with occasional hovers. Intra-specific harrassment was seen only in the context of one tern finding a fish and up to two others flying over and chivvying the gleaner. The gleaner held on to its fish in the four cases where this was observed. Twice, a patrolling tern rapidly switched its patrol track when a Puffin chased by Arctic Skuas passed nearby. These terns flew 'in the wake' of the Puffin chase, but well behind the main protagonists, apparently searching for dropped fish. Terns were also seen to fly over and circle sites where Lesser Black-backed Gulls had recently found fish. Up to four terns were seen simultaneously quartering different parts of a burrow area c 150 m by 100 m. All gleaned fish were carried to the nearby tern colony.

DISCUSSION

Kleptoparasitism in birds occurs most frequently among colonial seabirds and may evolve rapidly if the advantages of obtaining food in this manner outweigh those of other feeding

methods (Brockmann and Barnard 1979). I was not able to quantify the energetic cost and benefits of different tern foraging methods at the two study sites. The present note thus do not allow rigorous assessment of tern robbing behaviour. Nevertheless they do indicate how conditions at the two sites might lead to a feeding association between terns and Puffins.

A tern can obtain food at a Puffin colony by gleaning or by piracy. If the net energy gained by such foraging is greater than or equal to the energy which could be gained by fishing at sea, foraging at a Puffin colony could be an alternative or better feeding method for a tern than fishing at sea. I suggest that the choice of feeding method may be influenced by the density of fish on the ground, the density of fish-carrying Puffins at the colony, and competition for food with other species. Where kleptoparasitism by species other than terns over land is high, but the traffic of fish-carrying Puffins is low, one might expect gleaning to be the preferred feeding method. Piracy could be costly in comparison to gleaning since it uses energy to chase Puffins and compete with other pirates. Where kleptoparasitism by other species over land is low, and the traffic of fish-carrying Puffins high, piracy may be a better alternative, or additional feeding method to gleaning. Some support for this variation in strategy is provided by gleaning success at Vik and Mykines.

Both Puffin colonies described here are atypical. The Vik colony has an unusually high incidence of successful kleptoparasitic attacks on Puffins by species other than terns. More chases of Puffins by Arctic Skuas at Vik result in the Puffin dropping its fish load than in interactions between these species elsewhere (data in Andersson 1976, Arnason and Grant 1978, Furness 1978), possibly because Vik Puffins have less chance of escaping pirates than at sites nearer the sea (Grant 1971). The limited data presented here indicate that Arctic Terns at Vik gleaned a fish on just under half the patrols monitored; roughly once every four minutes of patrol time. Some Vik terns nested closer to the Puffin colony than to the sea. For such birds, gleaning at the Puffin colony might have been a profitable feeding method. Vik terns were never seen robbing Puffins.

In contrast to Vik, Mykines has a very high density of Puffin nest burrows and although skuas attack fish-carrying Puffins, these attacks take place over the sea. Fish dropped after successful skua attacks will thus be only briefly available for gleaning by other species before they sink. Terns on Mykines thus have access to unusually high densities of fish-carrying Puffins, but unlike Vik, only limited access to fish dropped as a result of piracy by other species. My notes suggest that gleaning was not a profitable feeding method for Mykines terns but that some piracy occurred. Nørrevang (1960) noticed terns fishing at sea near Mykines only on calm days and considered piracy to be the normal tern feeding method at the Puffin colony. Since the fishing ability of Arctic Terns can be adversely affected by increasing wind strength and rain (Bengtson 1966 and see Dunn 1973), Mykines terns may forage at the Puffin colony mainly when adverse weather makes fishing at sea difficult. My observations were made on days when wind strength was Beaufort force 4 or more, with frequent rain.

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SCOTTISH BIRDS

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Earlier colony attendance by Guillemots and Razorbills

K. TAYLOR and J. B. REID

(Plate 22)

Cliff nesting auks are now seen on their breeding ledges much earlier in the winter than formerly. How widespread is this new habit, what are its causes, and why do some colonies attract many more birds in winter than in summer?

Most Guillemots and Razorbills leave their breeding colonies in July and the rest at the beginning of August in Britain. Many Scottish Razorbills travel to Scandinavian waters in late summer and autumn, as do some Scottish Guillemots, but movements of Guillemots are still imperfectly known (Cramp *et al.* 1974, Mead 1974). While at sea after leaving the colony, moult of primary feathers renders Guillemots flightless for several weeks, but Razorbills may drop their remiges later than Guillemots (Birkhead & Taylor 1977). The birds return to the breeding site in winter, well before the onset of egg laying. The present study reviews information on the timing of this winter return for three colonies—Fair Isle, the Farne Islands and the Isle of May—where records are available from the 1950s to the 1970s (Bell 1962-6, *Birds in Northumbria* 1970-77, *Fair Isle Bird Observatory Reports* 1958-78, Isle of May Bird Observatory records, Eggeling 1974). Information from other areas is also presented to describe and assess the recent seasonal pattern of Guillemot and Razorbill colony attendance in the north of Britain. Population figures are quoted here in the units given by the counter.

Previous descriptions of colony attendance since the 1950s

In the 1950s Baxter & Rintoul (1953) recorded that Guillemots and Razorbills did not normally visit the breeding cliffs in Scotland until February. Bannerman & Lodge (1963) con-

sidered that while Guillemots 'exceptionally' came ashore in Britain in December, northern colonies were reoccupied after the turn of the year, with Razorbills landing in late February. About 1964, the pattern of Guillemot attendance on Fair Isle began to change, with birds being seen ashore in December and November between 1964 and 1967 (Dennis 1967). By the 1970s, winter records of Guillemots ashore were available from other Scottish colonies (e.g. Greenwood 1972), and Mead (1974) stated that some birds were at colonies in October. No similar trend of progressively earlier return to the breeding site was noted for the Razorbill, except that on Fair Isle they returned a few weeks earlier between 1964 and 1967 than was usual in previous years (Dennis 1967).

Attendance at Fair Isle, the Farne Islands and the Isle of May

The first recorded autumn and winter landings of Guillemots and Razorbills on Fair Isle are plotted as mean landing dates over three year periods from 1958-78 in fig. 1. There was a significant tendency for both species to return progressively earlier after 1963 (Spearman's rank correlation coefficient: Guillemot $r_s = -0.71$, $p < .01$; Razorbill $r_s = -0.57$, $p < .05$, $n = 15$). During this period the Fair Isle Guillemot population rose from 1,500-2,000 pairs in 1959 to 5,640 pairs in 1965 and c.10,000 pairs in 1969 and 1975. The Fair Isle Razorbill

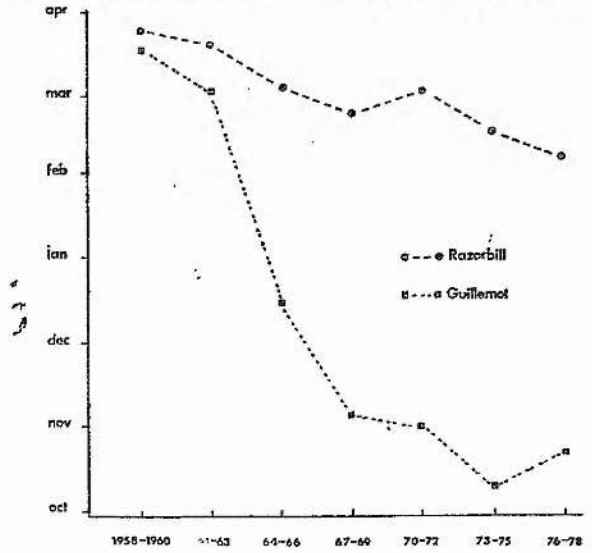

FIG. 1. Mean autum. /winter landfall dates for Fair Isle auks.

population increased from 750-1,000 pairs in 1965 to 1,200 pairs in 1969 and possibly 2,500 pairs in 1975 (Davis 1965, Cramp *et al.* 1974, Scottish Bird Report 1975).

The mean date Guillemots were last seen ashore on Fair Isle was 4th August (standard deviation ± 6 days) in the 1960s and 7th August in the 1970s. The mean date Razorbills were last seen ashore was 2nd August (s.d. ± 7 days) in the 1960s and 8th August (s.d. ± 7 days) in the 1970s.

On the Farne Islands records are dependent on dates of first observer visits to the colony. A comment that a return of Guillemots on 6th January 1952 was 'unusually early' should be viewed in this context (Watt 1953). Mean Guillemot return date was 14th November (s.d. ± 8 days) for 1961-5 and 3rd November (s.d. ± 11 days) for 1970-77. The Pinnacles colony increased from 1,300 pairs in 1971 to 2,400 pairs in 1977. Desertion of the Pinnacles occurs mainly in the first fortnight in August.

There are records of Guillemots and Razorbills ashore on the Isle of May in October, November and December since the 1950s. Our observations in 1978, and information in the observatory records, suggests that both species begin to visit the island in early October, the number of birds ashore increasing over the next few weeks, so that many thousands of Guillemots and several hundred Razorbills may be seen ashore by the end of October. Counts of these auks ashore on the Isle of May in autumn and winter 1952-79, together with approximate breeding population estimates for the fol-

Table 1. Autumn and winter Guillemot records, Isle of May

Date	No. ashore	Breeding pairs following season
1.11.52	c.50	2000
23.10.55	75	"
1.11.55	100	"
24.11.59	59	"
23.11.60	'many'	2000+
3.11.62	1000	"
1.11.64	1000+	"
24.10-25.11.66	2000+	"
5.10.70	170	"
2.11.70	2000	"
—.11.71	4400	3000-4000
—.12.72	4300	4000+
10.10.73	200	"
20.10.74	1200	"
23.12.74	16,000	"
14-17.10.75	400+	"
23.10.77	13,000	"
10-17.10.78	500+	"
23-30.10.78	'thousands'	"
17.10.79	1350	"

Table 2. Autumn and winter Razorbill records, Isle of May

Date	No. ashore	Breeding pairs following season
3.10.55	2	300-400
31.10.65	c.10	"
31.10-25.11.66	10+	"
5.10.71	100	"
—.11.71	800	"
10.10.73	65	400-500
23.12.74	500	"
14.10.75	50+	"
23.10.77	2000+	"
10-17.10.78	50+	"
23-30.10.78	1000	"
15.10.79	50	"

lowing breeding season, are shown in tables 1 and 2. In December 1974 and October 1977 the number of Guillemots ashore was in excess of the estimated breeding population on the island in the following breeding seasons. In October 1977 and 1978 the number of Razorbills ashore was also greater than the estimated breeding population. These recent pre-breeding season counts were made by observers who knew the size of the island's auk populations during the breeding season. Most Razorbills and Guillemots leave the Isle of May by the end of July.

Attendance at other colonies around Britain

There are only a few recent autumn and winter landfall records for Guillemots and Razorbills at other colonies in the north. In Shetland, Venables & Venables (1955) noted that Guillemots did not come ashore until early February, but recent records (*Shetland Bird Reports* 1969-77) include Guillemots on land in late December or January between 1969 and 1971, and from October from 1974 onwards. Shetland Razorbills, noted by Venables & Venables (1955) as making a landfall in the second week of March, were seen ashore in February from 1969 onwards. In Orkney, Guillemots were ashore in October 1971, and 'thousands' were on the Copinsay ledges in mid October 1977 (Scottish Bird Report 1971, Hope Jones 1978). In Caithness, Guillemots were ashore in December 1971 and November 1972 (Scottish Bird Reports 1971, 1972).

While attendance by Guillemots at English colonies from mid October onwards is now normal, autumn sightings of Razorbills ashore are unusual (T. Birkhead pers. comm.). Guillemots were ashore at Bempton in November 1870 (Cordeaux 1872). In Wales Guillemots have been seen ashore in December for many years (Fisher & Lockley 1954), but Razorbills do not come on land until later, such as those on Skokholm which usually return in March (Lloyd 1972, 1976). In Ireland Guillemots were ashore on Great Saltee in October 1955 and 1957 (*Irish Bird Reports* 1955, 1957). North of Britain there was a traditional belief among Faeroese seabird fowlers that Guillemots came ashore on the island of Skuvoy on 25th January (Norrevang 1977).

Discussion

The change in the pattern of Guillemot attendance on Fair Isle which began in 1964 was considered by Dennis (1967) to be associated with a local increase in small fish such as sandeels (Ammodytidae). *Ammodytes marinus*, one of the main prey of Guillemots, spawns in February and March in Scottish waters and has a major spawning ground around Orkney (Langham 1971). In 1965 a tenfold increase in the abundance of the young of spring spawning species such as sandeels was recorded in the western English Channel (Russell 1973). While this may have reflected a much broader change in marine populations in the Northern Hemisphere (Cushing & Dickson 1976), it is not known whether there were similar changes in the Orkney area at this time.

An increase in local food abundance might allow birds to moult near the colony and thus return early to the breeding site but does not by itself explain why birds should come ashore in autumn and winter. While food supply appears to be the ultimate factor controlling the phasing of the breeding cycle in many northern seabirds (e.g. Salomonsen 1955), intraspecific competition for nest sites may be an important proximate factor. Birkhead (1978b) showed that more intraspecific aggression occurred among Guillemots ashore from November to March than at other times and considered that this aggression was indicative of nest site competition. Such competition is more intense in the densely breeding Guillemot than in the relatively dispersed breeding Razorbill and may partly explain why Guillemots come back earlier to the breeding site.

The idea that early return of Guillemots to the breeding site is a result of pressure on nest sites is suggested by the Fair Isle data, where birds tended to return to the colony progressively earlier during a period when the estimated breeding population on the island increased fivefold.

Guillemots are flightless for 40-50 days during the post-nuptial primary moult, which takes about 63 days (Birkhead & Taylor 1977). Observations of Guillemots ashore at northern colonies in October, where most birds do not leave the ledges until late July or early August, suggest that some birds return

to the breeding ledges very soon after post-nuptial primary moult.

Proper interpretation of the significance of large numbers of auks ashore in winter on the Isle of May requires more accurate breeding population estimates than those made to date. Standard census methods are described by Birkhead & Nettleship (1980). Estimation of the ratio of breeding pairs to individuals present at the colony is of crucial importance in censusing cliff breeding auks (cf. Birkhead 1978a). In the absence of a ratio for the Isle of May it is not possible to say whether winter counts in excess of the estimated breeding population indicate that the island is used by auks from other colonies at this time of year. At one Guillemot colony on Skomer (Wales) where the ratio was accurately estimated, the number of birds ashore at times of peak attendance in the pre-laying period was slightly greater than double the number of pairs later breeding there (Birkhead 1977). Since recent Isle of May winter counts give Guillemot numbers ashore three to four times greater than the estimated number of pairs later breeding there, the need for more rigorous censusing in summer, as well as winter, is obvious. Although it is possible that the counts included non-breeders and immatures, there are unlikely to be enough present in the population to explain the large discrepancy. There are few data on the geographical spread of colonies that have auks ashore in winter, and, as previously noted by Bourne & Dixon (1974), a lack of information on changes in numbers of birds ashore at single colonies in winter.

More counts should be made of Guillemots and Razorbills at the breeding colonies in winter, evidence presented here suggesting that observers could fruitfully begin studying many Scottish colonies from early October onwards. Winter counts have conservation importance, since large pre-breeding aggregations of auks, such as on the Isle of May during the winter, mean that an oil spill could be more damaging in winter than in the breeding season.

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Summary

Over the last two decades the seasonal pattern of colony attendance by Guillemots and Razorbills at some colonies in the north of Britain appears to have changed. Both species are now seen ashore earlier in winter than was previously considered normal. On the Isle of May both species have been seen as. ore in October since the 1950s. The recent pattern of attendance is documented for several colonies where records of autumn and winter auk visits are available. There is a scarcity of winter information for most other northern auk colonies. Early return to the colony may be due to intra-specific competition for nest sites, progressively earlier return to Fair Isle after 1963 being associated with an increase in the island's breeding populations. It is unlikely that the birds could come ashore much earlier than recorded to date since they are flightless for a period before this while moulting the primary feathers. There is a need for more, and more detailed, observations of Guillemots and Razorbills ashore at their colonies outside the breeding season. Winter auk counts could have conservation importance, but proper interpretation of such counts will require rigorous censusing of breeding populations.

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PLAYFUL INTERACTIONS BETWEEN RESIDENT HERRING GULLS *LARUS ARGENTATUS* AND MIGRATING BIRDS OVER THE ISLE OF MAY

Behaviours classed as play can be viewed as energetically costly in the short term, but ultimately beneficial by increasing the adult animal's capacity to perform sophisticated behaviours through 'practise'. The following observations on interactions between young Herring Gulls *Larus argentatus* and migrants (mainly thrushes—Turdidae) are interpreted as play. I suggest that, in this case, the skill practised was kleptoparasitism. On the other hand, previous observations of Herring Gulls (of unspecified age) attacking and killing exhausted migrant turdids off the east coast of Britain (Hobbs 1959) suggest that the interactions observed could, in some cases, represent practise in predation.

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From 11 to 16 October 1978 there was a sizeable passage of continental migrants over the Isle of May, Firth of Forth, Scotland. Migrants arrived from the North Sea in flocks (mean flock size 24·9±18·77, $n = 40$) which usually fragmented over the island, with some birds alighting briefly while others flew on west. Birds which landed did not feed, and those watched invariably took off heading west within five minutes of landing. At peak passage on 12 October *c.* 80% of the migrants were Redwings *Turdus musicus* and *c.* 20% Song Thrushes *Turdus philomelos*. Counts made over three separate 10-minute periods indicated that on average 2700 birds were passing per hour between 11.00 and 15.00 hrs (BST).

On 12 October I noticed a party of 15 young Herring Gulls *Larus argentatus*, aged from one to three years, gliding above the island's West Cliffs. As each new party of thrushes crossed the cliffs, some gulls would harry the migrants using various tactics. Normally, two or more gulls would chase separate individual thrushes for a few seconds, shallow diving above the birds before wheeling back to the cliff. In fewer cases, one gull would prolong its pursuit by segregating the migrant from its flock and causing it to crash dive towards the sea. On several occasions two or more gulls were seen to harry a single migrant. Such combined pursuits usually ended with all but one gull giving up after a few seconds and the remaining gull engaging in a prolonged chase. Some pursuits were terminated by inter-gull harassment.

The migrants carried no obvious food items, and in six hours watching during 12–16 October I saw no direct gull/migrant contact, yet some of the gulls' behaviour resembled kleptoparasitic chasing. For example, in many instances migrants which occupied peripheral flock positions were preferentially selected for chasing, such selective attacks resembling the behaviour of many adult predators (see, for example, Hamilton 1971). Combined chases, in which all but one gull would normally pull back from pursuit, are suggestive of the gulls' monitoring the cost-effectiveness of escalated chasing in a manner partly analagous to the behaviour of adult kleptoparasites such as Arctic Skuas *Stercorarius parasiticus* (Arnason & Grant 1978).

Other behaviour was not so refined. On one occasion a gull stooped into the centre of a tight flock of *c.* 90 thrushes, possibly risking wing damage by so doing. Also, some gulls began chases when their quarry was already 50 m or more ahead of them, and despite vigorous chasing were unable to close on their 'target'.

By the end of the main passage on 16 October, target birds had included Redwings, Song Thrushes, Blackbirds *Turdus merula*, Fieldfares *Turdus pilaris*, and Skylarks *Alauda arvensis*. Parties of finches, mainly Bramblings *Fringilla montifringilla*, were not molested, suggesting that the gulls may have been using a search image in their playful attacks.

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